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JAIME HINTON: LETTER FROM A RABID PLANT COLLECTOR IN MEXICO

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ABSTRACT

Excerpts of a letter from Jaime Hinton to B.L. Turner are reproduced to illustrate some recent plant collecting experiences in México.

KEY WORDS: México, plant collecting, Hinton

The literature is replete with accounts of early plant collectors in North America, especially México, along with their trials and tribulations (*e.g.*, Berlandier 1805-1851; Seemann 1825-1871; Pringle 1838-1911; etc.). Indeed, George B. Hinton (1882-1943), the father of Jaime Hinton whose exploits are touted here, was a renowned collector of Mexican plants; much of the senior Hinton's activity has been chronicled by Hinton & Rzedowski (1972; J. Arnold Arb. 53:141-181).

These early Mexican collectors were an unusual breed, often risking (and sometimes losing!) their lives in the hope or realization that their discoveries in the field might enrich all of botanical science, to say nothing of the long-time legacy of their exploits, resulting eponymy, or whatever. In those bygone days when practically every plant collection stood at least a fifty-fifty chance of being undescribed, the impetus for collecting in remote, previously unvisited areas, must have been irresistible to many, if not most.

But what about modern collectors? Have they outlived the perils of collecting, the sense adventure and discovery that accompanies the field worker on a sortie to some out-of-the-way site (albeit only 10-50 kilometers along a dirt road from some paved major highway)? Obviously not, to judge by a recent letter written to me by Jaime Hinton, giving an account of his and his son's attempt to collect in the remote mountainous regions of Nuevo León, México. One might argue that "the hunt" of present day collectors has never been more exciting, simply because what is expected in the way of novelties is drastically reduced. Thus the reward of discovery is vastly enhanced, not to mention the knowledge and sense of intellectual responsibility that the educated, environmentally informed collector must feel as he treads the few remaining wilderness

areas looking for a last survivor of man's pernicious onslaught upon pristine habitats, most of this brought on by the senseless rampant reproduction of mankind and the consumptive consumerism that accompanies such activity, a consumption eating at the well springs of biodiversity everywhere.

George Hinton, his son Jaime and his grandson George represent three generations of plant collectors in Mexico, all avid students of that nation's flora. I never met the deceased member of this trio, but I know personally and correspond erratically with the second and third generations, both zealous collectors like their forefather George. Since this "introduction" is largely meant to accompany excerpts from a letter written by Jaime, I will digress here to attempt some encapsulation of Jaime Hinton's physiognomy, personality, character, and style.

Jaime is a wiry, resilient man about 5 feet 10 inches tall with the gait of a western cowhand, what with his certain, unobtrusive, strides and his ambience of belonging to his particular territory. A Mexican citizen, but of British parents, green-eyed and greying at the temples, he first walked up to me wearing a large Tarascan sombrero and a wisp of smile, extending his hand, "Prof. Turner, I assume," eyeing my newly married quite lovely wife Gayle (25 years or more younger than either of us) as if she might be a remarkable flower to be plucked precariously off some Mexican bluff given the odd discovery, wherever. Good sensible man, I thought, excellent tastes. And, later, settling down as his guest at Rancho Aguililla, I marveled at his conversational abilities about plants, architecture, peoples, commerce, and world affairs. He was a consummate scholar and litterateur, and as to bearing he reminded me right off as a protagonist from one of John Huston's westerns, "Treasure of the Sierra Madre", perhaps. Whatever; I was enthralled. Later my wife said, "An attractive man, Jaime", I knew then that his peripheral glances were properly catalogued.

The day after our first meeting Jaime insisted that the two of us take a short field trip to the mountains east of Cerro Potosí. He took off in his souped-up Ford at 100 plus miles per hour. Truly, the fastest I'd ever traveled in an automobile. When I tactfully complained at the speed ("What's the rush?") he grinned, like Socrates might have, given the same admonition from his friends about sipping too fast his extract of hemlock, and responded "Hell, I can't wait to get in the field, not much time left in the day", or something like that, as if I too were wrapped up in his provocative enthusiasm. Anyway, he slowed down to 95 or so for the rest of the paved road, then down to 50 on dirt, and finally lurched to a stop high up in the hills along an overgrown semitropical gully, taking off upslope like a botanist bewildered, collecting what was in flower or fruit, commenting on environmental degradation, the catholic condition, confessions, confusions, whatever. Ten years older than me, perhaps, he was clearly better shod with a better bridle.

But on to a single long excerpt, from his most recent letter, which I repro-

duce here with his permission. And only over protestations of a sort: he would not wish ostentation or advertisement. I responded, "Me neither, but future generations ought to know the tribulations of plant collectors working in this part of our century, how they knew absolutely that this was their last chance to do something meaningful for mankind's intellectual pursuits, that someone cared about what once was here, please ...."

He relented and the excerpts follow.

> Dear Billie: June 25, 1993
>
> .... We're hard at work in El Viejo, where we notice quite a few species that were new when we collected them at other places not so long ago. But we still hope to find some interesting things, especially some of those intriguing little orchids named by Carol Todzia. Once done with El Viejo, then I can sell the four-wheel drive, and buy a delightful smooth-riding turbo. Would you believe it that our roughriding gasguzzling fourwheeldrivingsonofabitch got stuck up at Agua León last week–for a mere eighteen galling hours. Finally, through slipping and skidding, the sob wound up at the edge of an abyss, and I was sorely tempted to pull out the stones we had under the other three wheels, and let the sob go. However, we were out in the middle of no where, and the insurance people had recently paid me for a total-loss on a four-wheel-driving Ramcharger, so we finally got a tackle with three woodsmen, and tied to a treetrunk actually pulled the damn truck sidewise from the abyss, until I could coast down to a niche and turn around. But I think it does an old fart good to have the shit scared out of him now and then, Billie, don't you agree? Afterwards, at least for a time, an ordinary life seems by comparison quite enchanting.
>
> This last trip, from which I returned last night, showed me the colossal difference adequate chains can make on a sob. (Fourwheeldrive = sob). Due to rampaging rainstorms, no lumber trucks had been on the move for eleven days, so the whole range of El Viejo was my preserve. I hate meeting those trucks coming down the mountain, and having to back up a mile or two on the steep scary tracks before they can pass, with thousand-meter drops nudging me. Then, if C's with me, I turn the truck over to him for a while.
>
> Incidentally, before the rains began, while El Viejo was dry as tinder, a forest fire broke out on the summit, burned fifteen days, and consumed the whole top of the mountain (utterly free of grazing) before it was finally put out by a hundred men, including Federal Troops. Supposedly, the fire was started by lightening, which is often blamed for our forest fires. But as you well know, we don't have forests like those of Oregon and British Columbia,

where you have impossible jumbles twenty-feet deep of new and ancient humus. Our forests are open, park-like, and I think they are almost always deliberately set on fire by one Miguelito, who invariably blames "un trueno" for the fire. As you may recall *Mathiasella bupleuroides* was a dominant species on the heights of El Viejo, which led me to solemnly promise Dr. Constance some seed. But now that it's utterly gone, what'll I do about my solemn promise? As the Jamaicans say–sheeeeeit, man? Maybe you could tell Dr. Constance that I didn't get his seed because I broke my ass, or something. (Kidding aside, though, I've found a few Mathiasella's down below, and hope they'll produce some seed for Dr. Constance–if the peripatetic asshole goat don't beat me to them.)

We've been trying to get a permit to collect and send herbarium specimens abroad, and we seem, strangely enough, to be on the right track. Among other things, I pointed out to the Lords of Inexorable Reason, that there are only about thirty botanical collectors in all Mexico. Assuming that each collector makes twenty trips a year, which is a lot, and assuming that at each trip each collector takes ten kilos of specimens, which is again a lot, (and without dwelling upon the fact that much collecting is a matter of pruning, which increases growth), we have 6,000 kilos of vegetation, a mere six tons of herbarium specimens a year. On the other hand, we have thirty-six million head of cattle, three million horses, and twenty-one million goats, sheep and pigs, for a total of sixty million grazing beasties. Assuming that half of these are properly taken care of in adequate grazing lands, which is a lot, and that the other half are turned out to graze the national territory helterskelter, we have thirty million cows, horses, goats, sheep and pigs eating not forage crops but everything in sight, including a coupe of tourists from Topeka, Kansas. Each of these miserable mangy starving shambling slutty slattern shabby shitty shiftless shameful sore-assed animals consumes at least ten kilos of vegetation per day, or a yearly 3,650 kilos, for a total of a hundred and eighty two million tons a year. Now, I ask you, Billie, with the aid of your trusty computer and other secret methods you no doubt have at your distinguished disposal, if you were a bush, a tree, a terrestrial orchid, or even an untouchable German tourist, what do you think would do more damage to our flora, thirty collectors bringing home, along with a moldy piece of pork crackling they gnawed at but didn't finish for lunch because of three broken teeth, six selected tons of herbarium specimens a year, or having thirty million mangy starving shitty shabby shady screwly sheddy sore-assed cattle chomping their way, just prior to dropping dead

of inanition, blind staggers, aids and Almyer's disease, chomping their way through a hundred and eighty-two million tons of assorted but unsustaining vegetation? I can tell you honestly, Billie, that at this question, rhetorical as it might seem to you and Guy, I could see a blush of shame mingled with a new and corruscating enlightenment dawning upon the faces of our honorably distinguished bureaucrats. Now, before you accuse me of slovenly thinking, by acidly pointing out that I've skipped both the not inconsiderable multitudes of donkeys and mules ravaging our countryside, let me hasten to assure you, Billie, that I'm saving both donkeys and mules as weapons of last resort. In case I ever find myself on the losing end of the argumentative stick, supposing some enlightened bureaucrat were to advance a disquisition to the effect that botanical collectors consume not ten but ten thousand kilos a trip, I could providentially throw the donkeys and mules into the gap, and still come out a winner of the scrap. But where would you place the emphasis? With the six tons of herbarium specimens we discriminating mortals collect each year, or with the hundred and eighty-two million tons devoured by our wretched scurvy scrounging scurrilous shitty cattle? Put a starving cow into a mixed forest, and what chance of survival does anything lower than a tree have? Off some trees, they'll even eat off the bark, girdling the trees as they die of hunger. ....

Kindest personal regards to you both.
Jaime

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KARYOTAXONOMIC STUDIES ON WILD ECUADORIAN TUBER-BEARING *SOLANUM*, SECT. *PETOTA*

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ABSTRACT

A taxonomic and distributional summary is presented for the tuber-bearing potatoes of Ecuador.

KEY WORDS: *Solanum*, Solanaceae, Ecuador, karyotaxonomy

After the recent monographic publications on Bolivian potatoes (Hawkes & Hjerting 1989; Ochoa 1990), the tuber-bearing *Solanum* from Ecuador are some of the least known in sect. *Petota*, subsect. *Potatoe*. In the present paper, the author gives a brief summary of the Ecuadorian wild potato species as a result of his explorations and field works made in Ecuador, as well as his observations of living plants in CIP's experimental plots, and laboratory research. Exceptions, however, are *S. baezense* Ochoa (series *Conicibaccata*), *S. andreanum* Baker, and *S. serratoris* Ochoa (series *Tuberosa*), of which I did not have living material. Likewise, although I have made some herbarium collections, I have not included in this treatment and will not include in any of my further work, *S. juglandifolium* Dun. and *S. ochranthum* Dun. (series *Juglandifolia*).

Data given are mainly on the morphology of the species, habitat, geographical distribution, and my determinations on the chromosome number ($2n$) and the Endosperm Balance Number (EBN).

These studies have also been complemented by examinations of exsiccatae collected in the past by other authors and presently housed in European, and North and South American herbaria.

The wild tuber-bearing species studied here have been taxonomically grouped in series. If identified synonyms are known, these are given for each species.

I. *Solanum* series *Acaulia* Juz., Bull. Acad. Sci. U.R.S.S., ser. Biol. 2:316. 1937 (*nom. nud.*); *ex* Buk. & Kameraz, *Bases of Potato Breeding.* 21. 1959.

Solanum albicans (Ochoa) Ochoa, Phytologia 54(5):392. 1983. BASIONYM: *Solanum acaule* Bitt. var. *albicans* Ochoa, Agronomía, Lima 27:363-364. 1960. *Solanum acaule* Bitt. subsp. *albicans* (Ochoa) Hawkes, Scott. Pl. Breed. Rec. 117. 1963.

Plant small, rosette, short stem, very hairy, white hairs. Leaves 3-4 pairs of leaflets without or with few interjected leaflets. Corolla rotate, white or violet. Tubers round to elongate, 2-3 cm long, white.

Distribution: This species was found for the first time in Atocsaico, located in the Jalcas of Porcón at 3450 m alt., Province and Department of Cajamarca, northern Perú. Collections in Ecuador were made in Cerro Quilua, 3600 m alt. in route from Cerro Colorado to Carihuayrazo, Province Chimborazo and in Romerillo, ca. 3900 m alt., Canton Ambato, Province Tungurahua, under the V.n. of *Curiquinga.* Both collections have, as do the Peruvian *Solanum albicans*, $2n$ = 72 chromosomes and EBN = 4. This species is highly resistant to frost (-5°C).

II. *Solanum* series *Conicibaccata* Bitt. *in* DC., *Prodr.* 13(1):33. 1852.

Solanum albornozii Correll, Wrightia 2:178-179. 1961.

Leaves with numerous interstitial leaflets and (4-)5-6 pairs of folioles shortly petiolulate, glabrous or glabrescent, dark green and subvernicose above, puberulent in the lower surface, margins slightly revoluted. Corolla rotate-pentagonal, white above, white with a pale violet strip on the back of each petal. Berry typically long-conical. Chromosome number: $2n$ = 24, EBN = 2.

Distribution: So far it is collected only on the route from Loja to Catamayo, 2300-2600 m alt., Province Loja, Ecuador; mostly in humid thickets or bushes.

Solanum calacalinum Ochoa, Darwiniana 23(1):227-231. 1981.

This rare species is principally characterized by its small branched plant, very long stolons (1.5-2.0 m); small tubers 2-4 cm), white, oval to round. Leaves glabrous, 3-4 pairs

of leaflets with long petiolules (15-20 mm), 0-1(-2) pairs of interjected leaflets. Corolla rotate to rotate-pentagonal, very showy, large (4 cm). Berry long-conical with obtuse apex, 2.5 cm long. It is very susceptible to the attack of *Phytophthora infestans* and to the potato leafroll virus (PLRV). Chromosome number: $2n = 24$.

Distribution: Very restricted, so far it has been found only on Mount La Sirena, 3000 m alt. and Sillacunga, 2900 m alt., a few km from Calacali, Province Pichincha, on slopes of stony soil, with very poor vegetation.

Solanum colombianum Dun. *in* DC. *Prodr.* 13(1):33. 1852.

Solanum colombianum Dun. *in* DC. var. *trianae* Bitt., Fedde Repert. Sp. Nov. 11:382-383. 1912.

Solanum dolichocarpum Bitt., Fedde Repert. Sp. Nov. 12:4-5. 1913.

Solanum colombianum Dun. *in* DC. var. *trianae* Bitt. f. *quindiuense* Buk., Suppl. 47, Bull. Appl. Bot., Genet., Pl. Breed. 225-226. 1930.

Solanum colombianum Dun. *in* DC. f. *zipaquiranum* Hawkes, Bull. Imp. Bur. Pl. Breed. & Genet., Cambridge. 112. 1944.

Solanum colombianum Dun. *in* DC. var. *meridionale* Hawkes, Bull. Imp. Bur. Pl. Breed. & Genet., Cambridge. 112-113. 1944.

Solanum filamentum Correll, Wrightia 2:174-175. 1961.

Solanum caquetanum Ochoa, Phytologia 46(7):495-497. 1980.

Although the type locality of *Solanum colombianum* is Tovar, Estado de Mérida, Venezuela, in the time of Dunal, author of this species, the present territory of Venezuela, Colombia, and Ecuador were integrated under one nation named La Gran Colombia; hence the epithet of *colombianum*. This species has 3-5 pairs of leaflets and 2-4 (-6) pairs of interjected leaflets. Corolla rotate to rotate-pentagonal, white to light bluish or to light purple. Tubers usually long-cylindrical or subcylindrical, up to 8 cm long and 2 cm thick. Berries long-conical to ovoid-conical, 3.5 cm long.

En route from Leito to Río Chico, Cordillera de Los Leones, Province Tungurahua, at 2870 m alt., in the edges of woods and shrubs, I found an abundant colony of *Solanum colombianum* ($2n = 48$) locally called *Papa de Monte* which must have great resistance to the attack of *Phytophthora*

infestans. Its leaves showed a type of hypersensitive reaction proper for hosts with the major genes of resistance (R) against late-blight. Small areas with cultivated potatoes in the vicinities, on the contrary, were almost destroyed by this fungus. Chromosome number: $2n = 48$, EBN = 2.

Distribution: More in Colombia than in Venezuela or Ecuador, especially in the provinces of Cundinamarca and Boyacá. In Ecuador, the author found this species mostly in Tungurahua Province. Living in cloud forest at 2500-3500 m alt.

Solanum chomatophilum Bitt. f. *angustifolium* Correll, Wrightia 2:180. 1961.

Leaves 4-5 pairs of folioles and numerous interstitial leaflets. Folioles narrowly elliptic-lanceolate to lanceolate with subacute apex. Calyx asymmetric with longer lobes than the typical form. Berries ovoid. Resistant to *Phytophthora infestans*. Chromosome number: $2n = 24$, EBN = 2.

Distribution: Provinces Napo-Pastaza, Azuay, and Carchi, Ecuador, and the highlands of Department La Libertad, Perú, occurs at elevations ranging from 2500-3200 m alt., usually in cold and wet shrubby areas.

Solanum paucijugum Bitt., Fedde Repert. Sp. Nov. 11:431. 1912.

Plant dwarf and bushy, 20-30(-50) cm tall, sparsely pilose throughout. Tubers white, ovoid, 2-3 cm long. Leaves 2-3(-4) pairs of leaflets with (1-)2-3(-5) pairs of interjected leaflets, terminal leaflet much longer than the lateral. Corolla rotate-pentagonal, 2.5-2.8 cm in diameter, lilac to purple. Berries long-conical, light green with 2-3 vertical darker stripes, 2 cm long. Although it has some affinities with *Solanum flahaultii* from Colombia, both species are quite different in plant habit, leaf shape, and dissection and details of flowers. Chromosome number: $2n = 48$, EBN = 2.

Distribution: Central Ecuador, mostly in the provinces of Bolívar, Cotopaxi, Tungurahua, and Chimborazo between 3000-4000 m alt., in cloud forest, wet thickets and grassy slopes of páramos.

Solanum tundalomense Ochoa, Ann. Cient., Univ. Agr., Lima 1(1):106-109. 1963.

Plant usually very tall, 3-4 m high, branched very sparsely pilose. Tubers small, 3-5 cm long, white, ovoid to long subcylindrical. Leaves (3-)4-5 pairs of leaflets, (0-)2-5(-7) pairs of interjected leaflets, leaflets elliptic-lanceolate or narrowly elliptic-lanceolate with acute or acuminate apex. Corolla rotate, white or white with pale violet stripes. Berries long-conical, 3.5 cm long. Although this species has affinities with *Solanum colombianum*, I consider them to be different species. Besides the ploidy level, they have substantial differences both in the shape of the corolla and calyx morphology. It is resistant to *Phytophthora infestans* but very susceptible to *Synchytrium endobioticum*. The chromosome number, cited formerly by the author for *Solanum tundalomense* (see Ochoa 1972, p. 75) as $2n = 24$, unfortunately was mistyped. Counts made in more than 20 accessions of *Solanum tundalomense* from Ecuador have given $2n = 72$, EBN = 4.

Distribution: Widely distributed in Ecuador (in 10 of 20 provinces) with the highest concentrations in the provinces of Azuay and Cañar, occurs at elevations between 1900-3600 m alt. In shrubby and forest vegetation.

III. *Solanum* series *Olmosiana* Ochoa, An. Cient. Univ. Agr. 3:33. 1965.

Solanum olmosianum Ochoa, An. Cient. Univ. Agr. 3:34-37. 1965.

So far, this is the only representative species of the series. Its main morphological characteristics are the shape and dissection of the leaf, 1-3 pairs of leaflets, the irregular and wide wings of the rachis extended all the way down to the petiole, leaves glabrous, corolla deeply stellate and white-cream, 2.0 cm in diameter, tubers white, oblong, 2-3 cm long, usually smooth. *Solanum olmosianum* was found for the first time in the margins of Olmos River, near El Sauce at 1640 m alt. in the Province and Department of Lambayeque, Perú. However, I have also found it in Tabla Rumi, at 2500 m alt., in the Province of Loja, Ecuador. The two mentioned collections have $2n = 24$ chromosomes, EBN = 2.

Distribution: Ecuador and Perú, in the lower inter-Andean valleys between 1600-2500 m alt., in shrubby thickets.

IV. *Solanum* series *Tuberosa* Rydberg, Bull. Torrey Bot. Club 51:146-147. 1924. *nom. nud.*

Tuberosa (Rydberg) Buk. (*sensu stricto*), *ex* Buk. & Kameraz, *Bases of Potato Breeding.* 18. 1959.

Andigena Buk. *ex* Buk. & Kameraz, *Bases of Potato Breeding.* 24. 1959.

Transaequatorialia Buk. *ex* Buk. & Kameraz, *Bases of Potato Breeding.* 21. 1959.

Vaviloviana Buk. *ex* Buk. & Kameraz, *Bases of Potato Breeding.* 18. 1959.

Andreana Hawkes, Bull. Imp. Bur. Pl. Breed. & Genet., Cambridge. 2:50. 1944. *nom. nud.*

Minutifolia Correll, Texas Res. Found. Contrib. 4:216-218. 1962.

Solanum burtonii Ochoa, American Potato J. 59(6):263-266. 1982.

Plant to near 1 m tall, sparsely pilose throughout. Tubers white, 2-3 cm long, ovoid. Leaves, 3-4 pairs of orbicular interstitial leaflets. Leaflets rugose, cordate at base shortly petiolulate, terminal leaflet broad ovate to elliptic-lanceolate. Corolla rotate, small, 2 cm in diameter, light purple-lilac outside with central petal streaks from the petal base to tip of acumens. Berry unknown but the ovary is pyriform. This hybridogenic species known with the vernacular name of *Papa de Monte* or *Papa Chavela* has $2n = 36$ chromosomes.

Distribution: Found only in Montes de Nahuasu, at 3400 m alt., between Monte Negro and Salado, just above and behind the small waterfall in front of the village of Baños. Living in cloud forest associated with trees (*Cedrela*, *Cecropia*, *Juglans*) and shrubs (*Chusquea*, *Lupinus*, several species of Melastomataceae, orchids and ferns).

Solanum correlli Ochoa, American Potato J. 58(5):223-225. 1981.

Plant tall, up to 2 m high, suffrutescent. Tubers usually moniliform. Leaves sparsely pilose, 3-4 pairs of leaflets, shortly petiolulate, (1-)2-3(-4) pairs of interjected sessile leaflets. Leaflets ovate to ovate-lanceolate. Calyx 5.5-6.0 mm with linear acumens 1.5-2.0 mm long. Corolla rather rotate-pentagonal than rotate, lilac, 3.0-3.5 cm in diameter. Berries ovoid to globose. Chromosome number: $2n = 24$, $\mathrm{EBN} = 2$.

Distribution: So far found only near the shores of the Angas River, to an altitude of 2700 m, Chimborazo Province. In margins of humid forests or shrubby thickets.

Solanum minutifoliolum Correll, Wrightia 2:191. 1961.

Plant stout, erect, usually 30-60 cm tall, densely pilose. Tubers ovate, white. Leaves subcoriaceous, dark green and coarsely pubescent on upper surface, pale green, finely pubescent on lower surface, 1-2(-3) pairs of elliptic-lanceolate shortly petiolulate leaflets and numerous to multiple several sizes of interjected leaflets, from (6-9-)11-20 (-26) pairs often minute, subimbricated and mostly suborbicular. Terminal leaflet broader and longer than the lateral. Peduncle densely hirsute. Corolla substellate, deep purple, 2.5 cm in diameter. Berries globose to slightly ovoid, 1.5 cm in diameter. It is quite resistant to late blight caused by *Phytophthora infestans*. Chromosome number: $2n = 24$, EBN = 1.

Distribution: Found in the provinces of Cañar, Chimborazo, and Tungurahua, occurs at elevations between 2800-3100 m alt., mainly in cloud forest, in shrubby thickets or margins of woods associated with ferns, orchids, *Fuchsia*, *Oxalis*, *Calceolaria*, Melastomataceae, and many Compositae.

Solanum regularifolium Correll, Wrightia 2:194. 1961.

Plant very simple, 50-70 cm tall, sparsely pubescent throughout. Tubers white-yellowish, round to ovate, 3-4 cm. Leaves 3-4(-5) pairs of leaflets without interjected leaflets, leaflets sessile to shortly petiolulate, elliptic to elliptic-lanceolate, apex subacute to obtuse, base mostly rounded and oblique. Corolla pentagonal, light blue with white acumens, 2.5-3.0 cm in diameter. Calyx strongly asymmetric, very pubescent, 7 mm long, linear acumens. Chromosome number: $2n = 24$. Very susceptible to *Phytophthora infestans* in plant and tubers.

Distribution: Very limited, I found it only near the type locality, south of Guasuntos, Iltus, en route Riobamba towards Cañar, 2400 m alt., Chimborazo Province. The collection *Correll & Smith P827*, made near Olmos on road to Jaen, Department Lambayeque, Perú, determined by Correll as *Solanum regularifolium*, in my opinion, belongs to *S.*

huancabambense Ochoa. The habitat of *S. regularifolium* is a narrow and very dry valley, with poor vegetation. I saw there only a few Gramineae and some trees of *Schinus molle* L.

Solanum suffrutescens Correll, Wrightia 2:183-184. 1961.

Solanum cyanophyllum Correll, Wrightia 2:180. 1961.

Plant shrubby, very branched, slightly pubescent. Stem subterete, slightly woody, strongly pigmented with reddish-brown. Tubers round or long subcylindrical up to 8 cm long and 1.5 cm thick. Leaves with narrow wings on the rachis, 3-4(-5) pairs of leaflets and (2-)5-7(-8) pairs of interjected decurrent leaflets, leaflets sessile to shortly petiolulate, elliptic-lanceolate with acute or shortly acuminate apex, base obliquely rounded. Calyx asymmetrical, narrowed lobes, linear acumens. Corolla rotate-pentagonal, 2.5-2.8 cm in diameter, deep purple to lilac, 2.5-3.0 cm in diameter. Berries ovoid to subglobose. Chromosome number: $2n = 24$, EBN $= 2$.

Distribution: In Ecuador, between Magdalena and Balzapampa, mainly in the hills of Samosurco and Pisco-urco, also in Panjor and Guamote, at 2600-3700 m alt., Bolívar Province. In wet thickets of valleys and near páramos in edges of woods, frequently associated with *Salvia*, *Calceolaria*, *Chusquea*, *Rubus*, Compositae, and several species of grasses.

V. *Solanum* series *Piurana* Hawkes, Ann. Mag. Nat. Hist., Ser. 12. 7:693. 1954.

Solanum chilliasense Ochoa, Lorentzia 4:9-11. 1981.

Plant about 1 m tall, glabrous or glabrescent throughout. Tubers small, round to ovate, 1.0-2.0 cm long, white. Leaves dark green and subvernicose above, light green and opaque below, 2-3 pairs of shortly petiolulate leaflets and (1-)2-3 pairs of interjected sessile leaflets; terminal leaflet widely elliptic to elliptic-lanceolate with acuminate apex, much larger than the laterals. Corolla rotate, lilac with white acumens, 1.8-2.5 cm in diameter. Berries ovoid, 1.5-2.0 cm long. This species presents a type of hypersensitive

reaction to the attack of *Phytophthora infestans*, therefore, it is highly valuable for potato breeding programs dealing with major genes of resistance (R). Chromosome number: $2n = 24$, EBN = 2.

Distribution: So far has been found only in the vicinities of Cordillera de Chilla, between Burro Urco and Chilola, at 3450 m alt., El Oro Province. Usually in cold foggy places or cloud forest among shrubby thickets or edges of woods.

Solanum solisii Hawkes, Bull. Imp. Bur. Pl. Breed. & Genet., Cambridge. 125-156. 1944.

Plant small, 30-40 cm tall, bushy, branched and rosette near base, glabrescent to sparsely pilose throughout. Tubers small, 1.0-3.0 cm, round and white. Leaves with little shine, 1-2(-3) pairs of sessile leaflets, usually without interjected leaflets, terminal leaflet larger than the laterals, elliptic to broadly elliptic-lanceolate, lateral leaflets elliptic. Corolla lilac (2.0-)2.5-3.5 cm in diameter, rotate with short and wide acumens with deep interpetalar notches giving an outline of multilobulate aspect. Berries ovoid to long-ovoid, 1.5-2.0 cm long.

Distribution: From central to south Ecuador, in the provinces of Tungurahua, Cañar, and Azuay, between 3500-4000 m alt., especially in thickets of high altitude páramos and grassy meadows.

Solanum tuquerrense Hawkes, Ann. Mag. Nat. Hist., Ser. 12. 7:693-697. 1954.

Plant robust, 50-60(-80) cm tall, glabrous or glabrescent throughout. Tubers long, cylindrical or subcylindrical up to 8 cm long, whitish. Leaves olive-green vernicose above, pale green and opaque below, (2-)3-5 pairs of slightly revolute leaflets, interjected leaflets few to many (1-2-)4-8(-11) pairs, sessile or decurrent on the narrowly winged rachis. Lateral leaflets broadly elliptic or ovate-lanceolate to narrowly elliptic-lanceolate with acute or shortly acuminate apex, subsessile. Terminal leaflet larger than laterals. Corolla rotate to rotate-pentagonal, blue-purple or violet purple, 2.5-3.5 cm in diameter. Berries long-ovoid to long-conical, 3 cm long and 1.7 cm broad. Chromosome number: $2n = 48$. EBN = 2.

Distribution: From Department Nariño, south of Colombia to the provinces of Carchi, Imbabura, Pichincha, Cotopaxi, and Napo in northern Ecuador at elevations between 3000-3450 m. Occurs in cold places, grassy meadows, wet thickets or edges of woods.

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TEXAS SPECIES OF *MIRABILIS* (NYCTAGINACEAE)

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ABSTRACT

A taxonomic treatment of the Texas species of *Mirabilis* (s.l.) is rendered. Thirteen species are recognized: *M. albida*, **M. austrotexana** B.L. Turner, *spec. nov.*, *M. comata*, *M. gigantea*, *M. glabra*, *M. hirsuta*, *M. jalapa*, *M. linearis*, *M. longiflora*, *M. multiflora*, *M. nyctaginea*, *M. oxybaphoides*, and **M. texensis** (Coulter) B.L. Turner, *comb. et stat. nov.* This stands in marked contrast with the most recent accounts of the Texas species rendered by Reed (1969) and Correll & Johnston (1970), both treatments recognizing 29 species. All of the names used by these authors are appropriately accounted for in the taxonomic treatment, and a key to the Texas species is provided, along with maps showing distributions.

KEY WORDS: Nyctaginaceae, *Mirabilis*, *Oxybaphus*, Texas

Mirabilis (sensu lato) is a New World genus of perhaps some 50 or more species, mostly confined to North America (Heimerl 1934). Standley (1909, 1911, 1918) and others after him, segregated from *Mirabilis* several natural groupings such as *Allionia* L., *Hesperonia* Standl., *Oxybaphus* L'Herit., and *Quamoclidion* Choisy, treating these as genera. But Standley (1931) recanted and reverted to Heimerl's generic concept, and most recent workers have tended to accept *Mirabilis* in the broad sense (*e.g.*, Pilz 1978; Le Duc 1993).

Mirabilis (s.l.) is well represented in the Texas flora, the most recent treatments recognizing 29 species (Reed 1969; Correll & Johnston 1970). Attempts to use either of the latter contributions is certain to induce taxonomic consternation of the most severe sort. This is largely due to the very superficial treatment accorded the group by Reed. His treatment placed considerable emphasis upon habit, leaf shape, and vestiture, characters which are very variable both within and between populations. He did little, if any, field work in connection with his study.

Indeed, Reed's treatment of *Mirabilis* for Texas is essentially unusable; his keys and annotations make little biological sense and, as noted in my comments under *M. austrotexana* B.L. Turner, one is left with the impression that he was not deeply involved with the taxonomic process in this instance, or else had little interest in providing a meaningful treatment with biological merit. It is unfortunate that Correll & Johnston chose to follow his treatment; this has caused a generation of workers, both professional and amateur, to throw up their hands in despair, myself included.

After many years of frustration in my attempts to identify *Mirabilis* species in Texas and northern México, I decided to start from scratch and work up the genus in this region based upon my own field experience, taxonomic concepts, and character analysis. In this I emphasized mainly fruit characters and placed relatively little emphasis upon leaf shape and vestiture. In addition, I attempted to relate morphological characters, whatever their nature, with ecogeographical variables. In short, an effort was made to recognize morphogeographical populational units that represent my best estimates of biological species. I was surprised and pleased by the results obtained. Instead of the 29 species proposed for Texas by Reed, only thirteen species seem deserving of specific status. This number might be increased to fourteen if one opts to recognize *Mirabilis dumetorum* Shinners, but if the latter is to be accepted it must bear a newly constructed name, *M. latifolia* (= *Allionia latifolia* [A. Gray] Standl.). *Mirabilis dumetorum* appears to be a broad-leafed form of the widespread exceedingly variable *M. albida* (Walt.) Heimerl, as noted under the latter.

The following key should prove useful in attempts to identify the thirteen species recognized here. In combination with the maps provided, relatively little difficulty should be encountered in understanding my taxonomic views regarding this group in Texas, or elsewhere.

KEY TO TEXAS MIRABILIS

1. Perianths 3-17 cm long. .... (2)

1. Perianths 1-2 cm long. .... (4)

  2. Involucres with 3-10 flowers. .... *M. multiflora*

  2. Involucres with 1 flower. .... (3)

3. Perianths 10-17 cm long, mostly white. .... *M. longiflora*

3. Perianths 3-6 cm long, variously pink to purple, rarely white. . *M. jalapa*

  4. Anthocarps ovoid, ribless, glabrous and essentially smooth; trans-Pecos. .... *M. oxybaphoides*

4. Anthocarps mostly ellipsoid, variously pubescent, or if glabrous then clearly ornate with ribs or tubercles. ....(5)

5. Anthocarps glabrous; stems stiffly erect, mostly glabrous and 1-2 m high; mostly sandy soils of northwestern Texas. ....*M. glabra*

5. Anthocarps to some extent pubescent, either pilose or short-glandular, mostly in silty or silty-clay soils (in sandy soils mainly in trans-Pecos, central, and southern Texas). ....(6)

6. Leaves linear to linear-lanceolate, mostly 2-10 mm wide; anthocarps conspicuously and rather evenly short-pilose, only a smattering of much shorter glandular hairs present, if at all. ....*M. linearis*

6. Leaves lanceolate to cordate, mostly 10-80 mm wide; anthocarps variously pubescent, but if so, the leaves ovate to cordate. ....(7)

7. Stiffly erect, simple-stemmed, robust herbs mostly 1-2 m high; mostly deep sandy soils of northcentral and southern Texas. ....(8)

7. Sprawling to erect herbs mostly 0.3-0.8 m high; mostly alluvial, silty clay in calcareous soils. ....(9)

8. Anthocarps conspicuously pubescent with a mosaic of mostly tufted hairs ca. 0.5 mm long; stems strigo-puberulent, hairs strongly upcurved and eglandular; northcentral Texas. ....*M. gigantea*

8. Anthocarps faintly pubescent with scattered pilose hairs ca. 0.3 mm long or less; stems pilose, hairs often glandular, or stems glabrous or glabrate; southern Texas. ....*M. austrotexana*

9. Anthocarps densely glandular-pubescent throughout with very short hairs; trans-Pecos. ....*M. texensis*

9. Anthocarps variously pubescent with well-developed eglandular pilose hairs, any glandular hairs much shorter and of secondary notability. (10)

10. Stem leaves sessile or nearly so, densely hirsute; northwestern Texas. ....*M. hirsuta*

10. Stem leaves various but usually to some considerable extent petiolate, glabrous to sparsely or moderately hirsute. ....(11)

11. Midstem leaves mostly 4-8 cm wide, the blades broadly obtuse, truncate or cordate at base; flowers mostly arranged in rather congested terminal clusters; northern Texas. ....*M. nyctaginea*

11. Midstem leaves mostly 1-4 cm wide, the blades gradually tapering upon the petioles, or abruptly truncate to cordate; flowers variously arranged but often in open divaricate corymbose panicles. .... (12)

  12. Leaves mostly cordate; involucres melanic, pubescent with uniseriate multiseptate trichomes, at least the cross-walls purplish or blackish in color; Franklin Mts., El Paso Co., rare. .... *M. comata*

  12. Leaves mostly lanceolate, broadly ovate to rarely cordate; involucres mostly not melanic, the trichomes with ± white or tawny cross-walls; widespread and common. .... *M. albida*

Mirabilis albida (Walt.) Heimerl, Ann. Cons. Jard. Geneve 5:182. 1901. BASIONYM: *Allionia albida* Walt. *Mirabilis nyctaginea* (Michx.) MacMillan var. *albida* (Walt.) Heimerl, *Oxybaphus albidus* (Walt.) Sweet

Allionia coahuilensis Standl. *Mirabilis coahuilensis* (Standl.) Standl. *Oxybaphus coahuilensis* (Standl.) Weatherby

Allionia grayana Standl. *Mirabilis grayana* (Standl.) Standl.

Allionia latifolia (A. Gray) Standl. *Oxybaphus nyctagineus* (Michx.) Sweet var. *latifolius* A. Gray

Allionia oblongifolia (A. Gray) Small. *Mirabilis oblongifolia* (A. Gray) Heimerl. *Oxybaphus nyctagineus* (Michx.) Sweet var. *oblongifolius* A. Gray

Allionia pseudaggregata (Heimerl) Weatherby. *Mirabilis pseudaggregata* Heimerl. *Oxybaphus pseudaggregata* (Heimerl) Standl.

Allionia rotata Standl. *Mirabilis rotata* (Standl.) I.M. Johnst.

Mirabilis albida (Walt.) Heimerl var. *lata* Shinners

Mirabilis dumetorum Shinners

Mirabilis entricha Shinners

Mirabilis muelleri Standl.

Mirabilis pauciflora (Buckl.) Standl. *Oxybaphus pauciflorus* Buckl.

As indicated by the above partial synonymy, and many more names not listed (*cf.* Reed 1969), *Mirabilis albida* is the most widespread highly variable species of *Mirabilis* in North America. This is probably due to its phenotypic plasticity and in large measure to its proclivity towards cleistogamic reproduction, presumably compounded by occasional hybridization with the many species with which it is sympatric. In any case, I accept a wide range of habit forms, leaf types, and vestiture in the complex. These various forms have been keyed and recognized as this or that species by Reed and yet others. But if

one examines carefully such plants they are very uniform as regards anthocarp shape, ornamentation, and vestiture. Characteristically, their anthocarps are markedly tuberculate, usually including the 4-5 ribs; at least to some degree, they are irregularly pubescent with tufted white hairs ca. 0.5 mm long; beneath the latter there is nearly always a minute layer of much shorter glandular hairs. Hairs of the latter type are not normally found in any large numbers on yet other species from Texas (for example, on anthocarps of *M. nyctaginea*, which has otherwise similar fruits to those of *M. albida*, nor are they found on fruits of *M. linearis* (Pursh) Heimerl, *M. glabra* (S. Wats.) Standl., or *M. austrotexana*, all of which might be confused with *M. albida* (given the aberrant individual among these). I am reasonably confident about my judgment with respect to the above treatment. I am, however, not especially sure of my relegation of *M. dumetorum* to synonymy. In spite of Shinners' certainty about its specific status, I believe what he has done is to select broad-leafed, pubescent-stemmed forms of otherwise typical *M. albida*, dubbing these *M. dumetorum*. For example, Travis County contains numerous sheets assignable to both *M. dumetorum* and *M. albida* by use of Shinners' (1951) key to species, but these do not appear to form discrete populational units. Indeed, various intermediate conditions in those characters states which purportedly distinguish between the species are found, suggesting that only a single variable taxon is concerned. Nevertheless, I might be wrong in this conjecture and, because of this, I have shown in Figure 1 the distribution of those leaf forms (by closed circles) which seem to conform to Shinners' concept of *M. dumetorum*. It will be seen that such plants occur over a broad region, but always confined within the broad distribution of *M. albida*.

In any case, if one accepts the biological reality of *Mirabilis dumetorum*, its correct name must be *M. latifolia*, as noted in my introduction to the present paper. The latter is based upon *Oxybaphus nyctagineus* var. *latifolius* A. Gray *in* Torr., *U.S. and Mex. Bound. Surv. Bot.* 174. 1859. TYPE: USA. Texas: Travis Co., near Austin, May 1849, *C. Wright 603* (LECTOTYPE [designated here]: GH!). Several collections were cited or referred to by Gray in his protologue. I have selected as lectotype one of two sheets bearing Wright's collection number *603*, both collected in the vicinity of Austin, Texas. The isolectotype is essentially sterile, while the lectotype itself has excellent fruiting material, the anthocarps are almost exactly like those of *M. albida*, both as to ornamentation and vestiture.

Mirabilis eutricha Shinners appears to be a form of *M. albida* with somewhat longer stem-hairs than is typical for the species. I believe that most of the other names listed in the above synonymy are reasonably certain, although I suspect that names applied to some of the Mexican collections might ultimately prove worthy of at least varietal recognition. Indeed, *M. comata* is very closely related to *M. albida*, and might be treated as a regional morphogeographical variety of the latter without much ado; I have retained the former

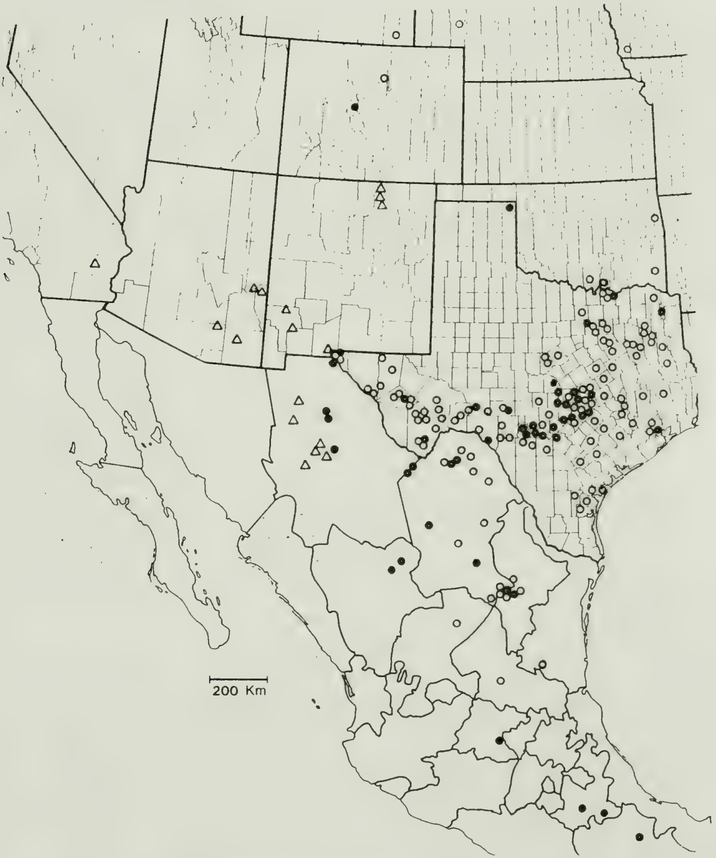

Figure 1. Distribution of *Mirabilis albida* and *M. comata* in Texas and closely adjacent areas: *M. albida*, leaves lanceolate to ovate (open circles); leaves ovate to cordate (closed circles); *M. comata* (open triangles).

as a species because it is largely allopatric with *M. albida* and undeniable intermediates at the periphery of their distributions have not been found so as to suggest varietal status.

Mirabilis austrotexana B.L. Turner, *spec. nov.* TYPE: U.S.A. Texas: Cameron Co.: Port Isabel, near the coast in sandy soil, 20 Nov 1964, *Robert Runyon 5831* (HOLOTYPE: TEX; Isotype: TEX).

Mirabili giganteae (Standl.) Shinners similis sed differt caulibus glabris vel pilosis trichomatibus patentibus saepe glandulosis (vs. rigide strigosis trichomatibus incurvatis nonglandulosisque et anthocarpis costis laevibus, inter costas sparsim pubescentibus trichomatibus minutis non caespitosisque (vs. costis nodosis, inter costas moderate pubescentibus trichomatibus caespitosis).

Stiffly erect robust perennial herbs mostly 0.8-1.5 m high. Stems mostly reddish brown, sparsely to densely pilose with spreading, often glandular, trichomes, rarely glabrous throughout. Midstem or lower leaves succulent, broadly lanceolate to ovate, sparsely pubescent to glabrous, mostly 6-12 cm long, 2-5 cm wide; petioles 0.3-2.0 cm long. Flowers arranged in terminal corymbose panicles 10-30 cm long, 10-15 cm wide. Fruiting involucres 8-12 cm across, 5-lobed, the lobes united for 1/2 their length or more. Flowers mostly 3 per involucre. Corollas rotate, mostly described as pink. Anthocarps mostly 4.5-5.5 mm long, 2.0-2.5 mm wide, about equally tapering at both ends, the 5 ribs mostly smooth and glabrous to sparsely short-pilose, between these the surface variously tuberculate, but nearly always bearing a collection of thin short-pilose hairs readily observable at 30-40×.

REPRESENTATIVE SPECIMENS (from among 40+ collections): U.S.A. Texas. Aransas Co.: dunes, ca. 300 yards back from Gulf, 31 Apr 1965, *Turner 5164* (NY,TEX). Atascosa Co.: ca. 10 mi N of Pleasanton in deep Carrizo sand, 6 Oct 1985, *Nesom 5203* (TEX); 4 mi NE of Pleasanton, 19 May 1980, *Turner 80-56M* (TEX). Bexar Co.: Essar Ranch, W of San Antonio, 2 Jan 1948, *Burr 227* (NY). Brooks Co.: 10 mi N of Encino, 16 Apr 1954, *Johnston 54500* (TEX); between Encino and United Carbon Black Plant, 16 Apr 1954, *Johnston 54500* (TEX); Falfurrias, 30 Nov 1951, *Tharp 52-561* (TEX). Cameron Co.: South Padre Isle, 3 Jun 1966, *Burlage s.n.* (TEX); dunes at mouth of Rio Grande, 10 Feb 1969, *Correll 36778* (LL); 5 mi W of Boca Chica, 2 May 1940, *Lundell & Lundell* (LL); Brazos Island State Park, 27 Aug 1977, *Richardson 2545* (TEX); same locality, 26 Nov 1977, *Richardson 2606* (TEX); clay dunes along Boca Chica Road near coast, 16 Jul 1935, *Runyon 3507* (TEX); Point Isabel, 29 Apr 1959, *Runyon 4669* (TEX). Jim Wells Co.: 2 mi S of Premont, 1-5 Aug 1921, *Ferris & Duncan 3249* (MO).

Kennedy Co.: near Rudolph, S of Norias, 3 Jan 1963, *Correll 26919* (TEX). Lavaca Co.: ca. 18 mi SE of Yoakum, 16 Jul 1949, *Tharp 49211* (TEX). Medina Co.: ca. 3 mi S of Devine, 28 Oct 1952, *Correll 15709* (LL). Willacy Co.: Yturria Station, 8 May 1949, *Runyon 4321* (TEX).

Reed (1969), both by citation and annotation, inexplicably treated this very natural populational complex from southern Texas (Figure 2) as belonging to six disparate species: *M. albida*, *M. dumetorum*, *M. exaltata* (Standl). Standl., *M. gigantea*, *M. nyctaginea*, and *M. oblongifolia*. As already noted, this was largely due to his emphasis upon habit, leaf shape, and vestiture. In short, he keyed and recognized states of these characters as representing species irrespective of their morphogeographical correlation with other characters.

Mirabilis comata (Small) Standl., Publ. Field Mus. Bot 8:306. 1931. BASIONYM: *Allionia comata* Small. *Oxybaphus comatus* (Small) Weatherby.

Reed (1969) positioned this taxon in synonymy under his concept of *Mirabilis oblongifolia*. I treat the latter as synonymous with the widespread, highly variable, *M. albida*. The type of *M. comata* is from southwestern New Mexico and is part of a populational complex largely confined to Arizona, New Mexico and closely adjacent states, including México (Figure 1). The taxon is closely related to *M. albida* but is seemingly readily distinguished by its usually cordate, long-petiolate leaves, sprawling habit and involucral vestiture of mostly darkened trichomes, as noted in the key to species. Only a single collection has been examined from Texas (Franklin Mountains, El Paso Co., *Worthington 8472* [TEX]).

Mirabilis gigantea (Standl.) Shinners, Field & Lab. 19:177. 1951. BASIONYM: *Allionia gigantea* Standl. *Oxybaphus giganteus* (Standl.) Weatherby.

As noted by Shinners (1951) this is a well-marked taxon largely confined to loose sandy soils of north-central Texas (Figure 2). It was also retained by Reed (1969) who confounded its distribution by citation of specimens of yet other taxa. *Mirabilis gigantea* has the habit of *M. austrotexana* but the latter is readily distinguished by its vestiture and anthocarps, as noted in the key to species.

Mirabilis glabra (S. Wats.) Standl., Publ. Field Mus. Bot. 8:304. 1931. BASIONYM: *Oxybaphus glaber* S. Wats. *Allionia glabra* (S. Wats.) Kuntze

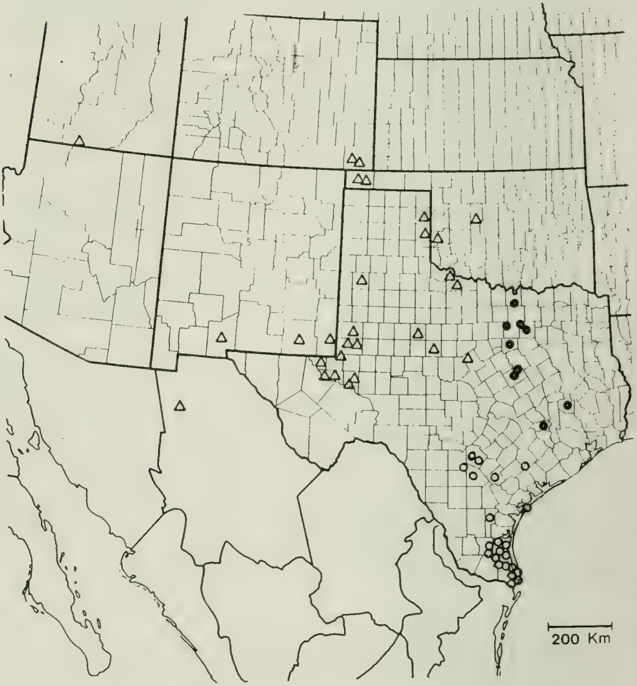

Figure 2. Distribution of *Mirabilis austrotexana* (open circles); *M. gigantea* (closed circles); and *M. glabra* (open triangles).

Allionia carletonii Standl.

Allionia ciliata Standl. *Mirabilis ciliata* (Standl.) Shinners.

Allionia exaltata Standl. *Mirabilis exaltata* (Standl.) Standl. *Oxybaphus exaltatus* (Standl.) Weatherby.

I cannot distinguish *Mirabilis exaltata* from *M. glabra*, although Reed (1969) and Correll & Johnston (1970) maintained both of these, distinguishing among them by relatively trivial features (mainly leaf shape and vestiture). Shinners (1951) also maintained *M. carletonii* and *M. exaltata* but notes that some of the former may "have pubescent fruits instead of glabrous ones". I presume that this observation was due to his misidentification of robust forms of *M. linearis* with *M. carletonii* (= *M. glabra*). In the *Flora of the Great Plains* (1986) it is noted that "Some specimens [of *M. glabra*] are difficult to distinguish from *M. exaltata* and we suspect intergradation." As already noted, I believe the two are indistinguishable. Its distribution in Texas and closely adjacent areas is shown in Figure 4.

Mirabilis hirsuta (Pursh) MacMillan, *Metasp. Minn. Valley* 217. 1892. BASIONYM: *Allionia hirsuta* Pursh. *Mirabilis nyctaginea* (Michx.) MacMillan var. *hirsuta* (Pursh) Heimerl. *Oxybaphus hirsutus* (Pursh) Sweet.

This taxon is recognized as a species with some reservation. Heimerl, as noted in the above (only partial) synonymy, treated it as a variety of *Mirabilis nyctaginea*, but I suspect that as treated by most American workers, it is a hodge-podge of hirsute specimens belonging to several species, mainly *M. albida* and *M. nyctaginea*. For example, Steyermark (1963), in his *Flora of Missouri* retained the species, but it seems clear from his key and distribution maps that it might be better treated as a leaf form of *M. albida*.

In the treatment of *Mirabilis* for the *Flora of the Great Plains* (Great Plains Flora Association 1986) *M. hirsuta* is said to be rare in Kansas and Missouri, and unreported from Oklahoma, but from my own map (Figure 4), it can be seen that forms referable to this taxon, as identifiable by their key, occur as far south as northern Texas and adjacent Oklahoma. In truth, I take such plants to be hirsute forms of *M. albida* but have mapped these as *M. hirsuta*. It should be noted that the specimens of *M. hirsuta* cited by Reed from Jeff Davis County, Texas are almost certainly hirsute forms of *M. albida*, both taxa occurring at the same site and apparently "intergrading" (*Hanson 506a-b* [LL,TEX]).

In short, *Mirabilis hirsuta*, if accepted as a biological entity, might best be treated within the *M. albida* complex, but its regional distribution, interpopulational variability, and typification needs additional study.

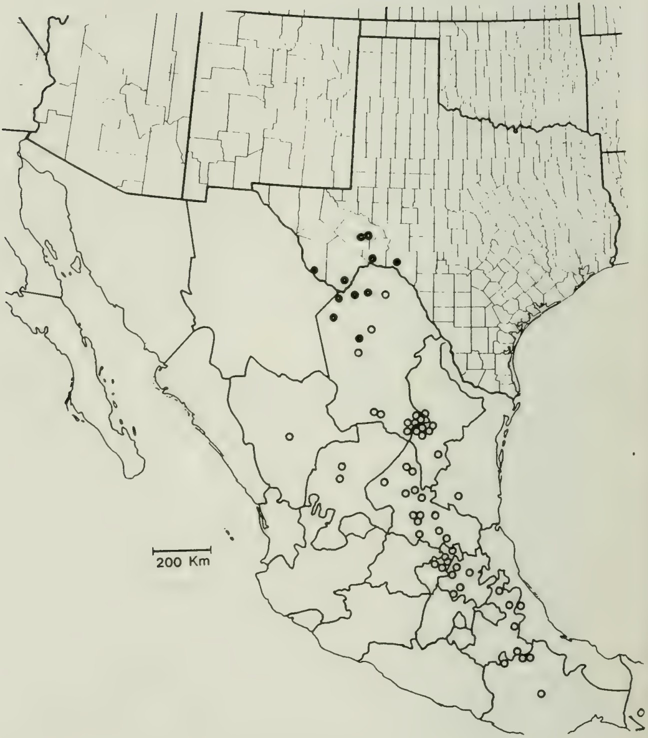

Figure 3. Distribution of *Mirabilis glabrifolia* (open circles) and the closely related *M. texensis* (closed circles).

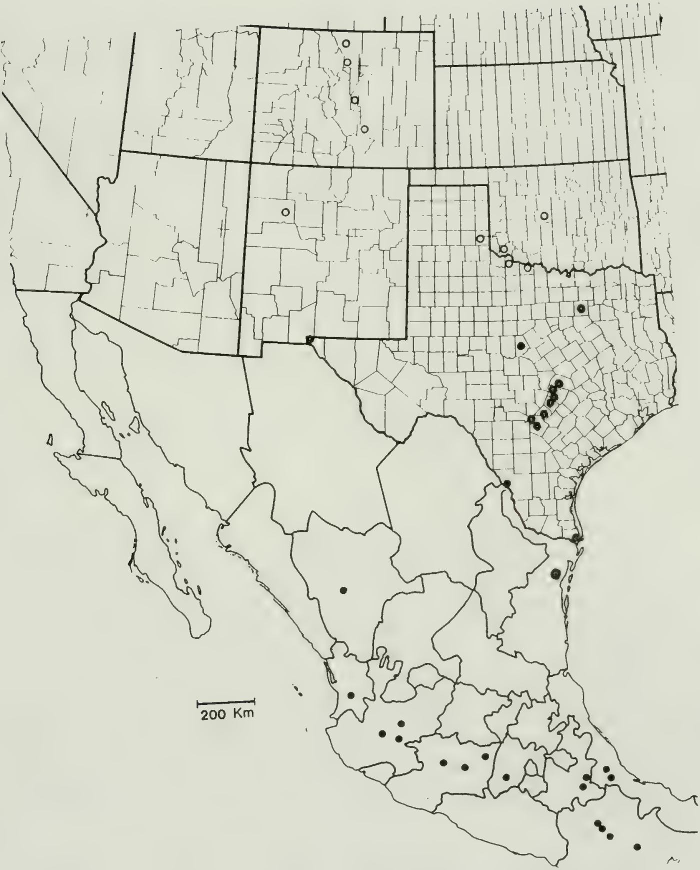

Figure 4. Distribution of *Mirabilis hirsuta* (open circles) and *M. jalapa* (closed circles) in Texas and closely adjacent areas.

Mirabilis jalapa L., *Sp. Pl.* 177. 1753.

Mirabilis jalapa L. var. *lindheimeri* (Standl.) Cory. BASIONYM: *Mirabilis jalapa* L. subsp. *lindheimeri* Standl. *Mirabilis lindheimeri* (Standl.) Shinners.

Shinners (1951), Reed (1969), and Correll & Johnston (1970) recognized both *Mirabilis jalapa* and *M. lindheimeri* as distinct species. Le Duc (1993), who monographed the subgenus *Mirabilis*, did not recognize infraspecific taxa under this widespread (Figure 4) highly variable, commonly cultivated species, many clones of which escape cultivation and persist.

Mirabilis linearis (Pursh) Heimerl, Ann. Cons. Jard. Bot. Geneve 5:186. 1900. BASIONYM: *Allionia linearis* Pursh. *Oxybaphus linearis* (Pursh) B.L. Robins.

Allionia decumbens (Nutt.) Spreng. *Calymenia decumbens* Nutt. *Mirabilis decumbens* (Nutt.) Daniels.

Allionia diffusa Heller. *Mirabilis diffusa* (Heller) Reed.

Allionia gausapoides Standl. *Mirabilis gausapoides* (Standl.) Standl.

Allionia vaseyi Standl.

As conceived here, this is a widespread highly variable taxon occurring over a broad region (Figure 5). It is sympatric with a number of other taxa and possibly forms the occasional hybrid with them. Reed (1969) and Correll & Johnston (1970) maintained *Mirabilis decumbens*, *M. gausapoides*, and *M. exaltata*; the first two appear to be decumbent and erect forms of *M. linearis* respectively, while *M. exaltata* (the type from Kansas) appears to be an unusually broad-leaved, pubescent-stemmed form with achenes essentially the same as found in typical *M. linearis*. It is likely that *M. exaltata* is of hybrid origin between *M. linearis* and *M. hirsuta*, the two taxa presumably occurring in close proximity upon occasion. Regardless, the anthocarps of all of these reputed species are seemingly identical, and are distinguished from those of *M. albida* (with which it might be confused in habit) by their relatively uniform short pilosity, and few, if any, much shorter glandular hairs beneath the pilose vestiture.

Mirabilis longiflora L., Köngl. Svenska Vetenska Acad. Handl. 176. t.6, 1755. *Jalapa longiflora* (L.) Moench

Texas material of this species belongs to the widespread *Mirabilis longiflora* var. *wrightiana* (A. Gray) Kearney & Peebles. The var. *longiflora* is largely

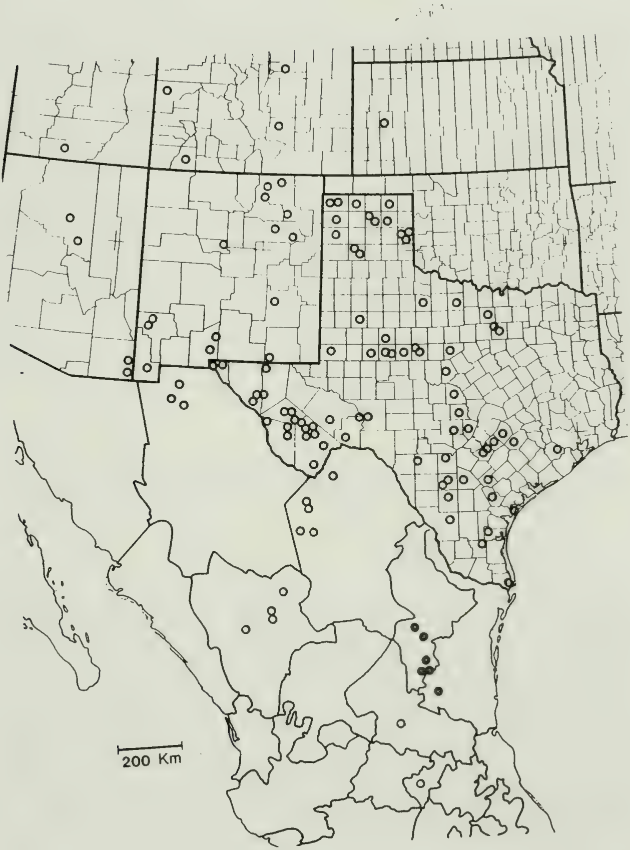

Figure 5. Distribution of *Mirabilis linearis* (open circles) and the superficially similar *M. nesomii* (closed circles).

restricted to southern México (Figure 6). Various workers have treated these two varieties as good species, but Le Duc (1993) maintained their varietal status.

Mirabilis multiflora (Torr.) A. Gray., *Bot. Mex. Bound. Surv.* 173. 1859. BASIONYM: *Oxybaphus multiflorus* Torr. *Quamoclidion multiflorum* (Torr.) Torr. & A. Gray.

Standley (1911) recognized this taxon, along with three others, as belonging to the genus *Quamoclidion*. In 1931, however, Standley repositioned the taxon in *Mirabilis*, following the treatment of Heimerl (1889). Heimerl (1934), in a definitive monograph, retained *Quamoclidion* in *Mirabilis*, as did Reed (1969).

Pilz (1978) has provided the most recent account of *Quamoclidion*, treating this as a subgenus of *Mirabilis* with six species, only one of which occurs in Texas, *M. multiflora*. Three more or less regional allopatric varieties of the latter were recognized by Pilz, ours belonging to the var. *multiflora*, which is confined to the trans-Pecos regions (Figure 7).

Mirabilis nyctaginea (Michx.) MacMillan, *Vetasp. Minn. Valley* 217. 1892. BASIONYM: *Allionia nyctaginea* Michx. *Oxybaphus nyctagineus* (Michx.) Sweet.

Mirabilis collina Shinners.

This widespread highly variable species, with its large somewhat sprawling habit, very large broadly ovate to subcordate leaves. and subfasciculate terminal inflorescence is rather easily recognized. In floral and fruit characters, however, it is very similar to *Mirabilis albida*, with which it is partially sympatric (*cf.* Figures 1 and 8).

Shinners (1951) thought *Mirabilis collina* to be "A very restricted endemic of the northwestern limits of the East Texas Pine Belt, suggesting a more delicate, more showy, and finely pubescent equivalent of *M. nyctaginea*; flowering rather early in the spring." Reed (1969) and Correll & Johnston (1970) retained the species. Shinners distinguished (in key form) *M. collina* from *M. nyctaginea* by vestiture (upper internodes pubescent or glabrous, lower internodes glabrous in *M. nyctaginea* vs. all internodes pubescent in *M. collina*), while Reed (1969) attempted to distinguish between these by mainly fruit characters (4 ribs in *M. collina* vs. 5 ribs in *M. nyctaginea*) and root-branching. In view of the considerable variation found in these characters, both within and between populations of *M. nyctaginea*, I have little hesitancy in treating *M. collina* as but a populational variant of the latter.

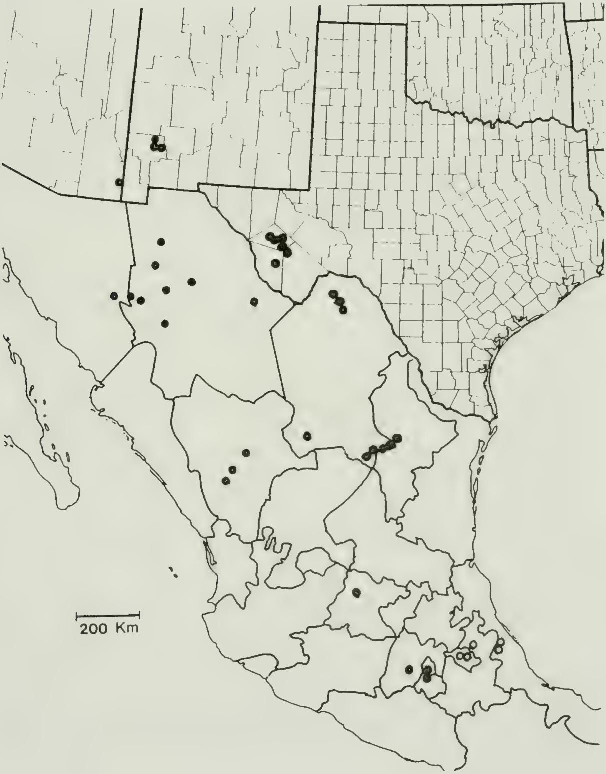

Figure 6. Distribution of *Mirabilis longiflora*: var. *longiflora* (open circles); var. *wrightii* (closed circles).

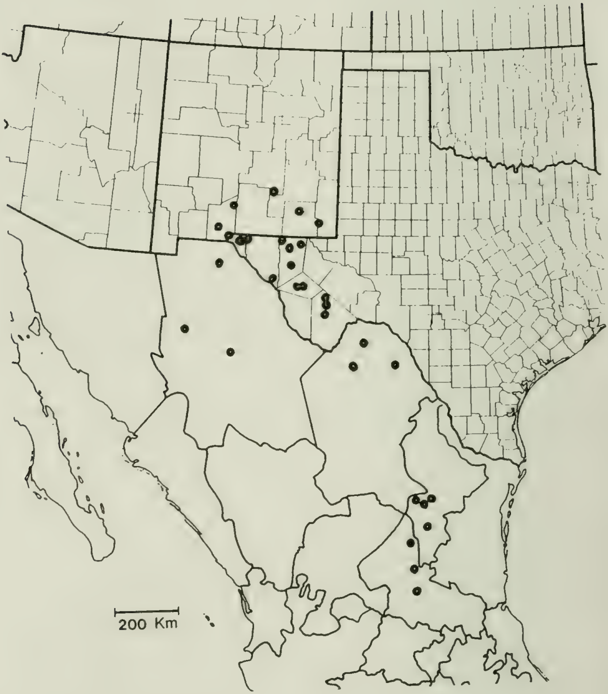

Figure 7. Distribution of *Mirabilis multiflora*.

Mirabilis oxybaphoides (A. Gray) A. Gray, *Bot. Mex. Bound. Surv.* 173. 1859. BASIONYM: *Quamoclidion oxybaphoides* A. Gray. *Allioniella oxybaphoides* (A. Gray) Rydb.

Oxybaphus wrightii Hemsl.

This taxon in Texas occurs only in the trans-Pecos (Figure 8). Early workers positioned it in the monotypic genus *Allioniella*, but most subsequent workers have positioned the species in *Mirabilis* (Heimerl 1934; Reed 1969; Correll & Johnston 1970).

Mirabilis oxybaphoides, in vegetative features, superficially resembles several species of *Mirabilis* in Texas, but is readily distinguished from all such by its smooth, glabrous ovoid achenes.

Mirabilis texensis (Coulter) B.L. Turner, *comb. et stat. nov.* BASIONYM: *Allionia corymbosa* Cav. var. *texensis* Coulter, Contr. U.S. Natl. Herb. 2:351. 1894. *Allionia texensis* (Coulter) Small, *Fl. Se. U.S.* 406. 1903. TYPE: U.S.A. Texas. Hudspeth Co.: north base of Eagle Mountains, 3 Sep 1849, *C. Wright 605* (HOLOTYPE: US!; Isotype: GH!).

Reed (1969) placed this taxon in synonymy with his concept of *M. glabrifolia* (G. Ortega) I.M. Johnst., to which it is closely related. Except for the type, all of the specimens cited by him belong to yet other taxa. *Mirabilis glabrifolia* is relatively widespread in México but does not occur in Texas. *Mirabilis texensis* is readily distinguished from the latter by its thicker, more uniformly cordate leaves. It is restricted to the Chihuahuan desert regions of western Texas and closely adjacent Coahuila, México, as shown in Figure 3.

ADDITIONAL NAMES RECOGNIZED BY REED FOR TEXAS AND NOT ACCOUNTED FOR IN THE ABOVE ACCOUNT

Mirabilis aggregata (Ort.) Cav.

This name was originally applied to Mexican material which I treat as synonymous with *Mirabilis glabriflora* Ort. The latter does not occur in Texas.

Mirabilis coccinea (Torr.) Benth. & Hook.

Reed listed this plant for Texas, but saw no specimens, nor have I. It is native to more western areas, mainly Arizona and closely adjacent states.

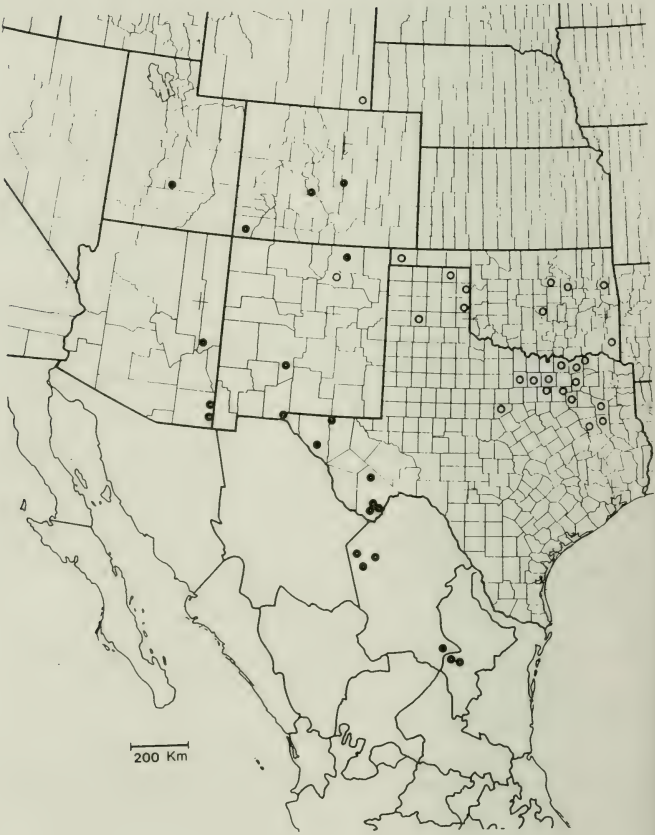

Figure 8. Distribution of *Mirabilis nyctaginea* (open circles) and *M. oxybaphoides* (closed circles) in Texas and closely adjacent regions.

ACKNOWLEDGMENTS

This study is based upon the study of approximately 1,000 specimens, mostly on file at LL, TEX. It was supplemented by the examination of critical collections and type specimens from GH and US. I am grateful to the latter institutions for the loan of these materials. Guy Nesom kindly provided the Latin diagnosis, and both he and Mark Mayfield reviewed the manuscript. Jackie Poole also read the paper and made helpful suggestions.

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TAXONOMY OF *DOELLINGERIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Doellingeria has most recently been treated within *Aster*, but it is here regarded as a distinct genus comprising eleven species. The five species of sect. *Doellingeria* are divided between eastern Asia (two species) and eastern North America (three species), while the six species of sect. *Cordifolium* are restricted to eastern Asia. The genus is hypothesized to be as closely related to *Solidago* and its relatives as to *Aster*.

KEY WORDS: *Doellingeria*, *Aster*, Astereae, Asteraceae

The genus *Doellingeria* was established by Nees (1832) and recognized by him as a group divided between North America and Asia. DeCandolle (1836) accepted *Doellingeria* as a distinct genus but restricted it to Asian species, inexplicably relegating the type (*D. umbellata* [Mill.] Nees) and other North American species to the genus *Diplostephium* Kunth. *Doellingeria* was accepted for a period during the 19th century, until Bentham (in Bentham & Hooker 1873) included it within a greatly expanded, heterogeneous *Aster*. Asa Gray maintained *Doellingeria* as a distinct genus in various treatments but finally submerged it within *Aster* in his *Synoptical Flora* (1884), deciding to adopt Bentham's view. Most North American botanists subsequently have subscribed in some degree to the concept of a conglomerated *Aster* advocated by Bentham and Gray, but some have continued to recognize *Doellingeria* as distinct (*e.g.*, Greene 1896; Rydberg 1917; Small 1933; Correll & Johnston 1970). Two recent studies of *Aster* in a relatively broad perspective (Jones 1980; Semple & Brouillet 1980) retained *Doellingeria* within *Aster*, although their justification for including it was not explicit.

The revisional study of *Aster* subg. *Doellingeria* (Semple *et al.* 1991) clarified the variation patterns of the North American taxa and their corresponding taxonomy, but the Old World taxa were not considered. Following an early judgment by Asa Gray (1884), recent treatments by Jones (1980), Semple &

Brouillet (1980), and Semple *et al.* (1983) have included *A. reticulatus* Pursh in subg. *Doellingeria*, but that species is here considered to lie outside the bounds of *Doellingeria* (see comments below).

Some Asian taxonomists have recently recognized the distinctiveness of *Doellingeria* (*e.g.*, Ling *et al.* 1985), but a number of "doellingerioid" Asian species have been retained within *Aster*. Tamamschyan (1959), apparently following DeCandolle, regarded the genus as monotypic, comprising only the Old World *D. scabra* (Thunb.) Nees. In China and Japan, where the greatest number of *Doellingeria* species occur, they have been treated either as *Aster* or *Kalimeris* Cass. (Kitamura 1936, 1937; Ohwi 1965; and literature citations below). Thus, *Doellingeria* as a genus has never been consolidated. The nature of the relationship between the Asian and American species of the genus apparently has only been considered by Bentham (in Bentham & Hooker 1873), who observed a strong relationship between the Asian *D. scabra* and the American *D. infirma* (Michx.) E. Greene.

As interpreted here, the boundaries of *Aster* do not encompass *Doellingeria*, which has ancestry closer to *Solidago* and related genera (comments below). *Doellingeria* comprises eleven species in two main groups: those of sect. *Doellingeria* have lanceolate, entire to serrulate, essentially epetiolate leaves, while those of sect. *Cordifolium* have ovate, coarsely toothed leaves with a distinct, narrowly winged petiole. There is a named hybrid (see below) between species of the two sections. Three species of sect. *Cordifolium* ser. *Cordifolium* have strongly foreshortened pappus and have been treated within the genus *Kalimeris*. Gu (1987, in press) excluded these species from *Kalimeris* but has not suggested an alternate placement for the group.

The five species of sect. *Doellingeria* are divided between eastern Asia and eastern North America, while the six of sect. *Cordifolium* are restricted to eastern Asia. *Doellingeria scabra* (sect. *Cordifolium*) occurs widely in eastern China, Japan, Korea, and northward into the Manchurian region of China and Russia; *D. marchandii* (Levl.) Ling and *D. longipetiolata* (Chang) Nesom (sect. *Cordifolium*) are endemic to southeastern China; and all of the other Old World species are restricted to Japan.

TAXONOMY OF *DOELLINGERIA*

Complete synonymy for the New World species is found in Semple *et al.* (1991); also see comments on nomenclature and typification in Jones (1980) and Reveal (1991).

Doellingeria Nees, *Gen. Sp. Aster.* 177. 1832. (TYPE: *Doellingeria umbellata* [Mill.] Nees).

Perennial, rhizomatous herbs, glabrous to sparsely strigose, eglandular. Leaves elliptic-oblanceolate or oblong-oblanceolate without an evident petiole to ovate-cordate with a long petiole, margins entire to coarsely toothed. Heads solitary on leafy peduncles, borne in a corymboid capitulescence; phyllaries in 2-4 weakly to strongly graduated series, broadly elliptic-oblong to ovate with a blunt or rounded apex, without a distinctly differentiated herbaceous tip, the midvein commonly slightly raised and resinous, often with conspicuous lateral nerves. Disc corollas abruptly broadened at the tube-throat junction, with long, reflexing-coiling lobes. Ray flowers few, the ligules white, not coiling with maturity. Achenes eglandular, otherwise sparsely strigose to glabrous, obovoid with 5-9, raised, broad, sometimes orange-resinous, equally spaced nerves or ribs, the achenes elongating at maturity to 3-4 mm long, nearly the length of the involucral bracts, raising the pappus almost completely above the involucre. Pappus 2-3-seriate, an outer series of setae or slender bristles much shorter than the inner, and much longer bristles in one or two inner series, all elements highly reduced in length in the three species of ser. *Cordifolium*; inner bristles with dilated apices. Chromosome number in all reported species of *Doellingeria*, n=9; secondary constriction of NOR chromosome in the middle of the short arm, the "primitive" type among various groups of *Aster* sensu lato according to Semple *et al.* (1983).

Key to the sections of *Doellingeria*

Pappus 3-seriate or 2(-3)-seriate; leaves entire, lanceolate, epetiolate or nearly so; eastern North America and eastern Asia. .... sect. *Doellingeria*

Pappus 2(-3)-seriate, sometimes prominently reduced in length; leaves coarsely toothed, ovate with relatively long, winged petioles; eastern Asia. .... sect. *Cordifolium*

A. *Doellingeria* sect. *Doellingeria*

Aster subg. *Doellingeria* (Nees) A. Gray, *Synopt. Fl. N. Amer.* 1(2):196. 1884. *Aster* sect. *Doellingeria* (Nees) Kitamura, J. Jap. Bot. 12:721. 1936.

Diplopappus sect. *Triplopappus* Torr. & Gray, *Fl. N. Amer.* 2:182. 1841. (TYPE: *Aster umbellatus* Mill.). *Aster* subg. *Doellingeria* sect. *Triplopappus* (Torr. & Gray) A.G. Jones, Brittonia 32:237. 1980.

Aster ser. *Sohayakienses* Kitamura, J. Jap. Bot. 12:722. 1936. (TYPE: *Aster sohayakiensis* Koidzumi).

a. *Doellingeria* ser. *Doellingeria*

1. *Doellingeria infirma* (Michx.) E. Greene, Pittonia 3:52. 1896. BASIONYM: *Aster infirmus* Michx., *Fl. Bor.-Amer.* 2:109. 1803.

   Doellingeria humilis (Willd.) Britt., *Britt. & Br. Illus. Fl.* 3:392. 1898.

   Aster cornifolius Muhl. *ex* Willd., *Sp. Pl.* 3:2039. 1803.

   Appalachian Mountains in eastern United States, northern Florida to New York and Massachusetts (see Semple *et al.* 1991, Fig. 16).

2. *Doellingeria sericocarpoides* Small, Bull. Torrey Bot. Club 25:620. 1898. *Aster sericocarpoides* (Small) K. Schum., Just. Bot. Jahresb. 26(1):375. 1900.

   Southeastern to south-central United States, North Carolina to Arkansas, southeastern Oklahoma, and east Texas (see Semple *et al.* 1991, Fig. 15).

3. *Doellingeria umbellata* (Miller) Nees, *Gen. Sp. Aster.* 178. 1832. BASIONYM: *Aster umbellatus* Miller, *Gard. Dict.*, ed. 8, no. 22. 1768.

   Aster amygdalinus Lam., *Encycl. Meth.* 1:305. 1783. *Doellingeria amygdalina* (Lam.) Nees, *Gen. Sp. Aster.* 179. 1832.

   Doellingeria umbellata (Miller) Nees var. *umbellata*

   Northeastern to east-central United States and immediately adjacent Canada (see Semple *et al.* 1991, Fig. 13).

   Doellingeria umbellata (Miller) Nees var. *pubens* (A. Gray) Britt., *Britt. & Br. Illus. Fl.* 3:392. 1898. BASIONYM: *Aster umbellatus* Miller var. *pubens* A. Gray, *Synopt. Fl. N. Amer.* 1(2):197. 1884. *Doellingeria pubens* (A. Gray) Rydb., Bull. Torrey Bot. Club 37:147. 1910. *Doellingeria umbellata* (Miller) Nees subsp. *pubens* (A. Gray) Löve & Löve, Taxon 31:357. 1982.

   Aster pubentior Cronq., Bull. Torrey Bot. Club 74:147. 1947.

   Northeast-central United States and immediately adjacent Canada, completely sympatric with var. *umbellata* (see Semple *et al.* 1991, Figs. 13 and 14).

4. **Doellingeria sohayakiensis** (Koidzumi) Nesom, *comb. nov.* BASIONYM: *Aster sohayakiensis* Koidzumi, Tokyo Bot. Mag. 37:56. 1923.

   Japan.

5. **Doellingeria rugulosa** (Maxim.) Nesom, *comb. nov.* BASIONYM: *Aster rugulosus* Maxim., *Mel. Biol.* 7:333. 1870.

   Japan.

B. **Doellingeria** sect. **Cordifolium** (Kitamura) Nesom, *comb. nov.* BASIONYM: *Kalimeris* sect. *Cordifolium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937. (LECTOTYPE, designated here: *Biotia japonica* Miq.).

Aster sect. *Teretiachaenium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:357. 1937. (LECTOTYPE, designated here: *Aster scaber* Thunb.).

b. **Doellingeria** ser. **Cordifolium** (Kitamura) Nesom, *comb. et stat. nov.* BASIONYM: *Kalimeris* sect. *Cordifolium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937. LECTOTYPE: *Doellingeria japonica* (Miq.) Nesom.

6. **Doellingeria japonica** (Miq.) Nesom, *comb. nov.* BASIONYM: *Biotia japonica* Miq., Ann. Mus. Bot. Lugduno-Batavum 2:170. 1866. *Boltonia japonica* (Miq.) Franch. & Sav., *Enum. Pl. Japon.* 1:226. 1875. *Asteromoea japonica* (Miq.) Matsum., *Shokub. Mei-i* ed. 2:41. 1895. *Aster japonicus* (Miq.) Franch. & Sav., *Enum. Pl. Japon.* 2:398. 1876. Not Less. *ex* Nees 1832. *Aster miquelianus* Hara [*nom. nov.*], J. Jap. Bot. 12:338. 1936. *Kalimeris miqueliana* (Hara) Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937.

   Japan.

7. *Doellingeria marchandii* (Levl.) Ling, *Icon. Cormorph. Sin.* 4:423. 1975. BASIONYM: *Aster marchandii* Levl., Fedde Repert. Sp. Nov. 11:306. 1912. *Kalimeris marchandii* (Levl.) Kitamura, Acta Phytotax. Geobot. 33:195. 1982.

   Widespread in southeastern China.

8. **Doellingeria longipetiolata** (Chang) Nesom, *comb. nov.* BASIONYM: *Aster longipetiolatus* Chang, Sunyatsenia 6:22. 1941. *Kalimeris longipetiolata* (Chang) Ling, *Fl. Reipubl. Pop. Sin.* 74:108. 1985.

   Aster trichanthus Hand.-Mazz., Oesterr. Bot. Zeit. 90:125. 1941.

   China, Szechuan province.

c. **Doellingeria** ser. **Papposae** Nesom, *ser. nov.*

Setae pappi longitudine corollas disci aequantes. TYPE: *Doellingeria scabra* (Thunb.) Nees.

9. *Doellingeria scabra* (Thunb.) Nees, *Gen. Sp. Aster.* 183. 1832. BASIONYM: *Aster scaber* Thunb., *Fl. Jap.* 316. 1784. *Eucephalus scaber* (Thunb.) Gandoger, Bull. Soc. Bot. France 65:40. 1918.

   Biotia discolor Maxim., *Prim. Fl. Amur.* 146. 1859.

   Widespread in eastern China, to Japan, Korea, and the Manchurian region of China and Russia.

10. **Doellingeria komonoensis** (Makino) Nesom, *comb. nov.* BASIONYM: *Aster komonoensis* Makino, Tokyo Bot. Mag. 12:65. 1898.

   Japan.

11. **Doellingeria dimorphophylla** (Franch. & Sav.) Nesom, *comb. nov.* BASIONYM: *Aster dimorphophyllus* Franch. & Sav., *Enum. Pl. Japon.* 1:224. 1875.

   Japan.

HYBRIDS:

Doellingeria sekimotoi (Makino) Nesom, *comb. nov.* BASIONYM: *Aster sekimotoi* Makino, J. Jap. Bot. 7:10. 1931. *Aster hashimotoi* Kitamura, Acta Phytotax. Geobot. 3:130. 1934. [*D. rugulosa* (Maxim.) Nesom × *D. scabra* (Thunb.) Nees; see Kitamura 1937, Ohwi 1965]

Japan.

EXCLUDED SPECIES:

1. *Doellingeria reticulata* (Pursh) E. Greene = *Aster reticulatus* Pursh.

2. *Doellingeria obovata* (Nutt.) Nees = *Aster reticulatus* Pursh.

   The alliance of *Aster reticulatus* with *Doellingeria* apparently has been on the basis of its corymboid capitulescence and other habital similarity and its tendency to produce a triseriate pappus. In *A. reticulatus*, however, the peduncles, phyllaries, and sometimes the leaves are glandular, the disc corolla lobes are erect and relatively more shallow, the achenes are fusiform and densely glandular, and the pappus bristles are apically acute. The species is an integral member of the group that includes *A. acuminatus* Michx. and *A. nemoralis* Sol. (Nesom in prep.).

3. *Doellingeria trichocarpa* DC., *Prodr.* 5:263. 1836. =? *Aster striatus* Champ. *ex* Benth. [*Fl. Hongkong.*], Hooker's J. Bot. Kew Gard. Misc. 4:233. 1852.

   Doellingeria trichocarpa was noted in *Index Kewensis* to be a synonym of *Aster striatus* Benth. The rationale for this is not clear, because Bentham (in Bentham & Hooker 1873) apparently accepted both species within the *Doellingeria* group of *Aster*. Judging from their descriptions, however, neither species can be interpreted as *Doellingeria* in the present view. Neither name has been included in *Aster* in relatively recent bibliographic and taxonomic accounts of the Chinese Compositae, but specimens at US originally identified as *A. striatus* have been annotated as *A. panduratus* Walp.

4. *Doellingeria ptarmicoides* Nees = *Oligoneuron album* (Nutt.) Nesom (Nesom 1993).

DEFINITION OF *DOELLINGERIA*

Doellingeria is recognized by its (1) corymboid capitulescence, (2) strongly graduated phyllaries with a blunt or rounded apex, without a distinctly differentiated herbaceous tip, with the midvein commonly raised and resinous, and often with conspicuous lateral nerves, (3) few ray flowers, the ligules not coiling with maturity, or at least coiling very little, (4) large, terete achenes with broad, often resinous ribs, and (5) a 2- or 3-seriate pappus of bristles with

dilated apices. The pappus in *Doellingeria* comprises one or two inner series of long bristles and an outer series of setae or slender bristles much shorter than the inner. The North American species have a consistently triseriate pappus, but within sect. *Doellingeria*, the pappus of the Asian *D. rugulosa* and *D. sohayakiensis* tends to be biseriate. The pappus in sect. *Cordifolium* also is mostly biseriate but the inner series tends to be congested or biseriate; the pappus is strongly reduced in length in ser. *Cordifolium*. The pappus bristles of the inner series in all species of both sections have dilated apices.

Doellingeria dimorphophylla and *D. japonica* differ between themselves primarily in relatively technical features of vestiture and the nature of their pappus. The pappus of the former (ser. *Papposae*) is composed of slender, apically dilated bristles 4-5 mm long in 2(-3) series; the pappus of *D. japonica* (ser. *Cordifolium*) is reduced to broad, flat, barbellate bristles 0.5-1.0 mm long, mostly lanceolate but sometimes with a distinctly clavellate apex. *Doellingeria marchandii* and *D. longipetiolata* have similarly reduced pappus, but the similarity between *D. japonica* and *D. dimorphophylla* in their particularly long stylar collecting appendages, which form 1/2-3/4 the length of the style branches, suggests that reduction of pappus may not be a reliable indicator of relationship among these species.

SUBTRIBAL PLACEMENT OF *DOELLINGERIA*

The phyletic position of *Doellingeria* is here hypothesized to lie near the base of the Solidagininae, near its point of divergence both from an Old World ancestor similar to *Aster* sensu stricto and from one group of New World *Aster* apparently closely related to the Solidagininae (*i.e.*, the "Biotian lineage", Nesom in prep.). The white rays and multiseriate pappus of *Doellingeria* are similar to true *Aster*, but the small number of ray flowers and eglandular, multinerved and more or less terete achenes are characteristic of the Solidagininae. White rays occur in other genera unequivocally placed among yellow-rayed Solidagininae (Nesom 1993) and they are invariably characteristic of the Biotian lineage. Disc corollas with deeply cut, reflexing-coiling lobes and pappus bristles with dilated apices occur in basal, yellow-rayed elements of the Solidagininae as well as the Biotian lineage. Correspondingly, the distinctive phyllaries of *Doellingeria* markedly resemble those of *Solidago* L., *Oligoneuron* Small, and the small group of species that has been treated as *Aster* sect. *Biotia* (DC.) Torr. & Gray (*e.g.*, Jones 1980).

Doellingeria was not included in the overview of the subtribe Solidagininae (Nesom 1993), but its morphology as well as its occurrence in eastern North America, with other primitive members of that subtribe, also suggest that the phyletic position of *Doellingeria* is in the same area. Although the radiation of the Solidagininae was primarily in North America, one of its most primitive

members (*Solidago*) has a distribution disjunct between North America and Asia. An analogous disjunction is hypothesized to occur between the southeast Asian endemic genus *Nannoglottis* Maxim., which also appears to be a primitive member of the Solidagininae, and the closely related, monotypic genus *Oreochrysum* Nutt. of the western United States (Nesom in prep.).

Jones & Young (1983, Figs. 4 and 5) placed *Doellingeria* as the sister group to the Eurasian genera *Galatella* DC. and *Crinitaria* Cass. (=*Linosyris* Cass.), but the latter two have glandular, flattened, primarily 2-ribbed, and obovate achenes and are more closely related to typical *Aster*. Plants of *Galatella* and *Crinitaria* also have a strong tendency to produce glandular-punctate leaves.

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VASCULAR FLORA OF SANDSTONE OUTCROP COMMUNITIES IN WESTERN LOUISIANA, WITH NOTES ON RARE AND NOTEWORTHY SPECIES

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ABSTRACT

The floristics and edaphic factors of west Louisiana sandstone outcrop communities are described. The soils of this open xeric community are moderately rich in calcium and support a number of calciphiles. Lichens and mosses are common, especially on the open rock pavement that characterizes this community. A number of rare species occur: *Talinum parviflorum*, *Schoenolirion wrightii*, *Carex meadii*, and *Selaginella arenicola* var. *riddellii*.

KEY WORDS: Sandstone outcrop, sandstone glade, calcareous prairie, cedar glade, calciphile, Kisatchie National Forest, floristics, Louisiana

INTRODUCTION

The eastern and southeastern United States is – or at least until recently was – heavily forested. Nonetheless, there were natural openings, usually of small size, scattered throughout. The more xeric of these openings – variously referred to as prairies, glades, and barrens – have long attracted the attention of naturalists, ecologists, and botanists, and there is a fairly large literature dealing with them (*e.g.*, Ebinger 1979; Perkins 1981; DeSelm 1986, 1990; Greller 1988; Baskin & Baskin 1989; Bartgis 1993).

In two previous papers, we have described sandstone glades in western Louisiana (MacRoberts & MacRoberts 1992, 1993). As our studies of open xeric communities in this area have expanded, we have become aware that there are at least two different types of sandstone related communities (MacRoberts & MacRoberts 1993). The type studied previously – referred to

as glade or sandstone glade – is an open area, often mesa-like, with acidic low-nutrient soils strewn with boulders and scattered with old, slow growing, stunted trees. The sandstone community described in this paper – referred to as sandstone outcrop or simply outcrop – while superficially similar to glades, is floristically and edaphically quite distinct. Among other things, these communities have a rock pavement or ledge, not boulders, upslope from which is open calcareous prairie-like habitat. An examination of the literature suggests that these openings most resemble cedar glades of Tennessee and Kentucky, and barrens in southeastern Texas (Baskin & Baskin 1975, 1985; Marietta & Nixon 1984; Bridges & Orzell 1989; Mohlenbrock 1993).

In this paper we describe outcrop communities in the Kisatchie National Forest in western Louisiana, an area for which such communities have not yet been described. We also compare these communities with the sandstone glades that we have studied previously, and briefly discuss calcareous prairies and forests in this part of Louisiana.

STUDY SITES AND METHODS

Three outcrops were selected for detailed study. All occur within 1 km of each other in T6N R8W, about 5 km north of Kisatchie, Louisiana, in the Kisatchie Ranger District of the Kisatchie National Forest (Caldwell 1991; Martin & Smith 1991). Two of these (KG30-3 and KG30-8) have large expanses of sandstone pavement. The third (KG30-2) does not, and while underlain by sandstone bedrock, has not eroded down to it except in a few small areas. Consequently, KG30-2 represents what can be considered an earlier stage in the evolution of this community. KG30-8 is about 0.4 ha, KG30-2 about 0.6 ha, and KG30-3 about 1.2 ha. All occur at approximately 75 meters above sea level.

Following Perkins (1981) we divide outcrops into life zones (Figure 1). These are 1) eroded area below the lip of the sandstone bedrock, 2) bare rock pavement, 3) pockets of shallow soil on rock pavement, 4) sloping prairie above pavement with soils of varying depth depending on distance from exposed rock and degree of slope, and 5) tree/shrub zone uphill.

Not all outcrop communities have all zones. In the three we studied, KG30-3 and KG30-8 had all zones; KG30-2 consisted almost exclusively of zones 4 and 5, with only small areas of 2 and 3. Also, zone 1 at KG30-2 was heavily treed and shaded the very narrow zones 2 and 3. Other outcrop sites in the Kisatchie District consisted of only zones 1, 2, and 3; zones 4 and 5 had been eroded away (Figure 1). Zone 1 is perhaps the most variable, as we attempt to depict in Figure 1. Almost all of these communities are on hillsides, not on hilltops. The few we encountered on hilltops were entirely eroded to bedrock, as indicated in Figure 1.

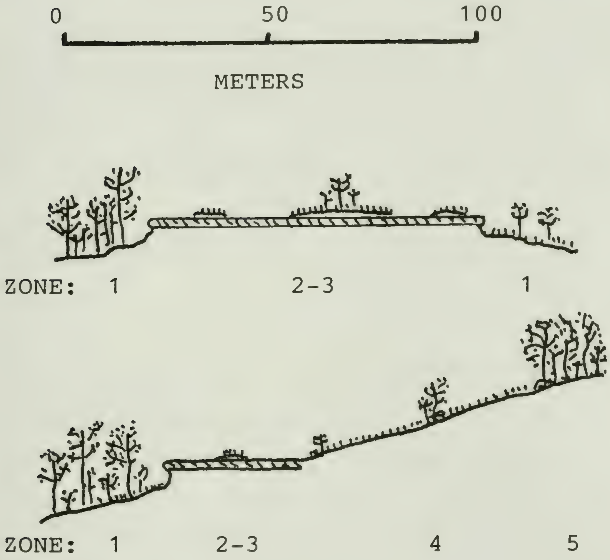

Figure 1. Profiles of typical outcrops with floristic zones indicated.

Table 1. Taxa of three sandstone outcrops.

AGAVACEAE – *Manfreda virginica* (L.) Rose.

AMARYLLIDACEAE – *Hypoxis hirsuta* (L.) Cov.

CYPERACEAE – *Carex caroliniana* Schwein., *C. flaccosperma* Dewey (2), *C. meadii* Dewey (2, 3), *Fimbristylis puberula* (Michx.) Vahl., *Rhynchospora inexpansa* (Michx.) Vahl., *R. globularis* (Chapm.) Small, *Scleria ciliata* Michx., *S. oligantha* Michx.

IRIDACEAE – *Sisyrinchium sagttiferum* Bickn. (2, 3).

JUNCACEAE – *Juncus marginatus* Rostk. (8).

LILIACEAE – *Aletris aurea* Walt., *Allium canadense* L., *Nothoscordum bivalve* (L.) Britt., *Schoenolirion wrightii* Sherman (3, 8), *Smilax* sp.

ORCHIDACEAE – *Platanthera nivea* (Nutt.) Luer (3), *Spiranthes lacera* (Raf.) Raf., *S. praecox* (Walt.) S. Wats.

POACEAE – *Agrostis elliottiana* Schultes (3, 8), *Andropogon tenarius* Michx., *Aristida longespica* Poir., *Aristida oligantha* Michx., *Aristida purpurascens* Poir. (2, 3), *Axonopus affinis* Chase (8), *Chasmanthium sessiliflorum* (Poir.) Yates (3), *Dicanthelium aciculare* (Desv. *ex* Poir.) Gould & Clark, *D. acuminatum* (Sw.) Gould & Clark (3), *D. sphaerocarpon* (Ell.) Gould, *Eragrostis elliottii* S. Wats. (8), *E. spectabilis* (Pursh) Steud. (2), *Muhlenbergia capillaris* (Lam.) Trin. (3), *Panicum anceps* Michx. (2, 8), *Paspalum notatum* Flugge (3), *Schizachyrium scoparium* (Michx.) Nash, *Schizachyrium tenerum* Nees, *Setaria geniculata* (Lam.) Beauv. (3), *Sporobolus junceus* (Michx.) Kunth (2, 3), *Vulpia octoflora* (Walt.) Rydb. (2, 3).

CUPRESSACEAE – *Juniperus virginiana* L.

PINACEAE – *Pinus echinata* P. Mill., *P. palustris* P. Mill., *P. taeda* L.

SELAGINELLACEAE – *Selaginella arenicola* Underw. var. *riddellii* (Eselt.) Waterfall (3).

ACANTHACEAE – *Ruellia humilis* Nutt.

APIACEAE – *Eryngium yuccifolium* Michx. (2).

AQUIFOLIACEAE – *Ilex decidua* Walt. (8), *I. vomitoria* Ait.

ASCLEPIADACEAE – *Asclepias longifolia* Michx., *A. viridiflora* Raf. (2, 3).

Table 1 (continued).

ASTERACEAE - *Aster dumosus* L., *A. linariifolius* L., *A. oolentangiensis* Ridd. (3), *A. paludosus* Dryand. *ex* Ait. ssp. *hemisphericus* (Alex.) Cronq., *A. patens* Ait. (2, 3), *A. sericeus* Vent., *Bigelowia nuttallii* Anderson, *Cirsium carolinianum* (Walt.) Fern. & Schub. (2, 3), *Coreopsis lanceolata* L., *Erigeron strigosus* Muhl. *ex* Willd. (2, 3), *Gnaphalium purpureum* L. (2, 3), *Helianthus angustifolius* L., *Heterotheca graminifolia* (Michx.) Shinners, *Krigia virginica* (L.) Willd. (3, 8), *Liatris aspera* Michx. (2), *L. earlei* (E. Greene) Schum. (2), *L. squarrosa* (L.) Michx., *Pyrrhopappus carolinianus* (Walt.) DC. (2), *Silphium laciniatum* L., *Solidago nitida* Torr. & Gray (2, 3), *Vernonia texana* (A. Gray) Small (2).

BIGNONIACEAE - *Campsis radicans* (L.) Seem. *ex* Bureau (3).

CAMPANULACEAE - *Lobelia appendiculata* A.DC., *Triodanis perfoliata* (L.) Nieuwl. (2).

CISTACEAE - *Lechea tenuifolia* Michx. (3).

CLUSIACEAE - *Hypericum gentianoides* (L.) B.S.P. (3, 8), *H. hypericoides* (L.) Crantz.

CONVOLVULACEAE - *Evolvulus sericeus* Sw.

CORNACEAE - *Cornus florida* L. (3).

DROSERACEAE - *Drosera brevifolia* Pursh (8).

ERICACEAE - *Vaccinium arboreum* Marsh., *V. corymbosum* L. (3, 8).

EUPHORBIACEAE - *Croton capitatus* Michx. (2), *Crotonopsis elliptica* Willd., *Euphorbia corollata* L., *Tragia urticifolia* Michx. (3).

FABACEAE - *Baptisia leucophaea* Nutt., *Crotalaria sagittalis* L. (2), *Dalea candida* (Michx.) Willd. (3), *D. purpurea* Vent. (3), *Galactia volubilis* (L.) Britt. (2, 3), *Medicago lupulina* L. (2), *Schrankia microphylla* (Dry.) J.F. Macbr. (2, 8), *Stylosanthes biflora* (L.) B.S.P., *Tephrosia virginiana* (L.) Pers.

FAGACEAE - *Quercus falcata* Michx. (2), *Q. marilandica* Muenchh., *Q. stellata* Wang.

GENTIANACEAE - *Sabatia campestris* Nutt.

HAMAMELIDACEAE - *Liquidambar styraciflua* L.

Table 1 (continued).

JUGLANDACEAE - *Carya* sp. (3).

LAMIACEAE - *Hedeoma hispidum* Pursh (2, 3), *Prunella vulgaris* L., *Salvia lyrata* L., *Scutellaria integrifolia* L. (2, 8), *Scutellaria parvula* Michx. (3).

LENTIBULARIACEAE - *Pinguicula pumila* Michx. (8).

LINACEAE - *Linum medium* (Planch.) Britt.

LOGANIACEAE - *Gelsemium sempervirens* (L.) St. Hil.

MYRICACEAE - *Myrica cerifera* L.

ONAGRACEAE - *Gaura* sp. (2), *Oenothera linifolia* Nutt. (3, 8).

OXALIDACEAE - *Oxalis stricta* L.

PLANTAGINACEAE - *Plantago aristata* Michx. (3), *P. virginica* L. (2, 3).

POLEMONIACEAE - *Phlox pilosa* L.

POLYGALACEAE - *Polygala nana* (Michx.) DC., *P. verticillata* L. (2, 3).

PORTULACACEAE - *Talinum parviflorum* Nutt. *ex* Torr. & Gray (3, 8).

RANUNCULACEAE - *Delphinium carolinianum* Walt. (3).

RHAMNACEAE - *Berchemia scandens* (Hill) K. Koch.

ROSACEAE - *Crataegus marshallii* Eggleston, *C. spathulata* Michx., *Prunus* sp. (3), *Rubus* sp. (2).

RUBIACEAE - *Diodia teres* Walt., *Hedyotis crassifolia* Raf., *H. nigricans* (Lam.) Fosberg (2, 3).

SCROPHULARIACEAE - *Agalinis fasciculata* (Ell.) Raf. (8), *Agalinis plukenettii* (Ell.) Raf. (3, 8), *Agalinis skinneriana* (Wood.) Britt. (2, 3), *Aureolaria pectinata* (Nutt.) Penn. (2, 3).

VERBENACEAE - *Callicarpa americana* L. (2), *Verbena halei* Small (2).

VIOLACEAE - *Viola pedata* L.

Table 1 is a list of the vascular plants found in zones 2, 3, and 4 of KG30-2, 3, and 8. The number "2" following the species indicates presence at KG30-2, "3" presence at KG30-3, and "8" presence at KG30-8. Absence of a letter indicates presence at all three sites.

We recorded a total of 136 taxa, representing 102 genera and 48 families for the three outcrops. KG30-3 had 110 species and 84 genera, KG30-2 had 101 species and 78 genera, and KG30-8 had 82 species and 65 genera, which makes these communities as rich in species as bogs (MacRoberts & MacRoberts 1992). Plant families with the greatest representation are Asteraceae, Fabaceae, and Poaceae, which account for 37% of the total. However, lichens and mosses, important components of the outcrop communities especially in zones 2 and 3, are not included here.

The three outcrops are similar. Among them, Sorensen's Index of Similarity ranges from 74 to 78. Combining all plants from sandstone glades (MacRoberts & MacRoberts 1992, 1993) and from sandstone outcrops, and comparing these lists, shows that glades and outcrops are not the same community. Sorensen's Index of Similarity between them is 49.

We visited all three study sites every two weeks from March to mid-November 1993 to collect and identify plants. Although these communities are rich in lichens and mosses, we did not attempt to identify them. We follow MacRoberts (1984, 1989), Gandhi & Thomas (1989), and Allen (1992) in most instances for botanical nomenclature. Voucher specimens of many of the species collected are deposited in the Vanderbilt University Herbarium (VDB). While the specific fire history of outcrop communities is uncertain, they are embedded in the pyrogenic longleaf pine community and thus probably burned with regularity in the past (Martin & Smith 1991; Smith 1991). The study sites had not burned in several years. Soil samples were taken from all zones at each study site and from all zones of a number of other outcrop communities from several calcareous prairies, and from one calcareous forest. The samples were analyzed by A & L Analytical Laboratories, Memphis, Tennessee.

To compare the spatial distribution and size of trees in outcrops with those in other communities, we ran transects through the middle of KG30-2, 3, and 8. This totaled an area 195 meters long and 3 meters wide (585 square meters). Within this area we mapped all trees over 1.5 meters tall and measured their diameter at breast height (dbh).

We cut at ground level four small pines (3 loblolly and 1 shortleaf) from zone 4 of KG30-3 to examine growth rings and thus growth rate.

We randomly selected ten temporary one meter square plots each in KG30-2, 3, and 8. Ten plots were in the thin soils on the pavement area (zone 3) and twenty in the deeper soils upslope (zone 4). In each we counted pine seedlings (first and second year trees) to see if pine establishment differed between glades and outcrops, and to determine why these communities remain open (see MacRoberts & MacRoberts 1993).

Using aerial photographs, we located 33 additional outcrop communities and surveyed each of these at least once, noting extent of sandstone pavement, erosion, flora, condition, typical and rare species, size, and other features. These surveys extended from February 1992 until December 1993.

Climatic data are given in Martin *et al.* (1990). Annual precipitation averages about 125 cm and is fairly evenly distributed throughout the year. In summer, temperatures rise to 35° C, which, combined with short droughts, translates into very hot and dry conditions, especially in open areas.

RESULTS

No vascular plant grew entirely on bare rock (zone 2); these areas were either bare or lichen covered. Lichens, mosses, and vascular plants occurred in zone 3. Depending on soil depth, there might also be a few very stunted pines or oaks. Lichens and mosses were found almost entirely in zones 2 and 3, and in the shallow soils between 3 and 4. When soil depth increased, lichens dropped out and were replaced by forbs and grasses, and by an occasional shrub. The few trees and shrubs growing in zone 4 usually occurred in scattered clumps. Zone 5 typically began abruptly as dense woods with heavy mid- and understory.

Table 2 gives soil characteristics of the various zones. We collected soil samples from nine outcrops. These represent all zones, but especially 3 and 4, notably near rare species such as *Schoenolirion* and *Talinum* (both occur in zone 3). In Table 2 we have combined and averaged also, soils from several outcrops. Soils for zone 4 are divided into two groups: 4a is the upper 15 cm; 4b is 0.5 m deep or deeper. The upper layer of zone 4 is dark grey to black, but changes to light grey or buff between 0.25 and 0.5 m.

It was abundantly clear prior to soil analysis that the vegetation in the outcrop openings was usually calciphilous, and that almost always in the immediate vicinity of outcrops there was calcareous forest and very occasionally remnant calcareous prairie. Species characterizing calcareous forest and prairie are *Aesculus pavia* L., *Andropogon* spp., *Apocynum cannabinum* L., *Aristida* spp., *Berchemia scandens*, *Bumelia lycioides* (L.) Pers., *Crataegus* spp., *Dalea* spp., *Gleditsia triacanthos* L., *Helianthus hirsutus* Raf., *Juniperus virginiana*, *Neptunia lutea* (Leavenw.) Benth., *Prunus* spp., *Ratibida pinnata* (Vent.) Barnhart, *Salvia azurea* Lam., *Schizachyrium* spp., *Schrankia microphylla* (Sm.) Macbr., and *Viburnum dentatum* L.

To have a standard by which to judge their soil properties and those of associated communities, we collected and analyzed soils from two well studied calcareous prairies (Carpenter Road Prairie and Coldwater Road Prairie, Smith *et al.* 1989) in the Winn Ranger District of the Kisatchie National Forest about 65 km northeast of our study sites. We also had soils analyzed from

Table 2. Soil characteristics.

		Exchangeable ions (ppm)				
Sample	pH	P	K	Ca	Mg	OM%
All Outcrops (Kisatchie District)						
Zone 1 (3)	5.5	5	91	2223	285	1.0
Zone 3 (15)	5.3	15	83	1193	250	1.6
Zone 4a (11)	5.4	6	102	2535	281	3.2
Zone 4b (2)	7.8	1	117	4780	346	1.0
Zone 5 (2)	5.3	14	134	3590	376	9.1
Specific Outcrops (Kisatchie District)						
KG30-2						
Zone 4 (2)	5.4	4	198	4290	459	3.8
KG30-3						
Zone 4 (1)	5.9	3	151	3910	326	3.3
Zone 5 (2)	5.3	14	134	3590	376	9.1
KG30-8						
Zone 4 (1)	4.8	7	87	720	272	2.3
Prairies (Winn District)						
Carpenter (3)	7.8	3	137	3667	51	7.4
Coldwater (2)	7.7	1	183	5145	73	7.0
Prairies (Kisatchie District)						
Ratibida (3)	7.7	3	182	7330	90	6.7
K50H (2)	7.8	1	174	6485	60	4.6
Calcareous Forest (Kisatchie District)						
K50C (1)	5.9	3	234	6530	308	8.7

Table 3. Tree species number and size on outcrops.

Species	No. on outcrops	Average dbh (cm) (range)	
Pinus palustris	7	14.9	(5.1-22.9)
P. taeda	12	6.2	(2.5-12.7)
P. echinata	2	17.1	(3.8-30.5)
Quercus marilandica	3	4.2	(2.5-7.6)

Table 4. Tree size.

Diameter class dbh (cm)	No. of trees
1-5	9
5-10	5
10-15	4
15-20	2
20-25	3
25-30	0
30-35	1

two calcareous prairie remnants (Ratibida Prairie and K50H Prairie) and one calcareous forest located near outcrops on the Kisatchie Ranger District. The number of samples collected and analyzed from each area, zone, and site is shown in parentheses in the table. The average is given where there is more than one sample.

The area in which we located outcrops during our survey is a band several miles wide that runs east-west across the entire Kisatchie District (a distance of about 30 km). This band appears to correspond with the Lena Member of the Fleming Formation, the chief characteristic of which is its "calcareous clays" (Gorat & Roland 1984).

It was not surprising therefore to find that the soil samples confirmed what the vegetation already told us. The soils were calcareous. In some places, we found narrow strata consisting of nothing but calcareous concretions frequently there were small calcium aggregations scattered on the surface and mixed throughout the soils. This admixture may account for the low pH and high calcium in the samples.

The Natchitoches Parish soil survey classifies the areas in which the outcrops occur as Kisatchie soils; that is, "fine, montmorillonitic, thermic Typic Hapludalfs" (Martin *et al.* 1990). With the exception of high calcium, they are identical in acidity and mineral contents to the soils of the sandstone glades we studied earlier (MacRoberts & MacRoberts 1992, 1993).

As the data in the table show, the soils in KG30-2 and KG30-3 are as calcareous as the soils in the calcareous prairies. While some differences exist between the outcrop soils and those described from the prairies, notably surface pH and magnesium, the calcium content is approximately the same.

Tables 3 and 4 give information on tree distribution in transects in outcrop communities.

A comparison of the data given in our previous papers (MacRoberts & MacRoberts 1990, 1993) shows that outcrops and glades are very similar in

the distribution and abundance of trees, and that they differ in a number of ways from bogs and pinewoods. In pinewoods there was one tree per 11 square m, in glades there was one tree per 23.5 square m, and in bogs one tree per 35 square m. We found that in outcrops there was one tree per 24 square m. In bogs, glades, and outcrops the trees are stunted and old growth. However, bogs lack oaks, which are common in both glades and outcrops. In outcrops, trees are almost entirely confined to zones 1, 4, and 5. Zones 2 and 3 lack sufficient soil for trees to survive.

In our previous study, we found that the growth rate of pines differed significantly among glades, bogs, and pinewoods. Trees in glades grew at the slowest rate, averaging 11.5 rings per cm; bogs came next with 8.6 rings per cm; and trees in upland pinewoods had 3.7 rings per cm. The growth rate of pines from KG30-3 zone 4 was intermediate between bogs and glades, with 10.75 rings per cm (the four trees had 11, 11, 11, and 10 rings per cm). While this sample is small, it is unlikely that a larger sample would significantly alter the results since the trees in outcrops – as in bogs and glades – are clearly under stress (stunted, gnarled, and with scanty foliage).

In the outcrop communities, pine seedlings were absent in zone 2 and scarce in zone 3. In the ten one m square plots we examined in zone 3, there were only two seedlings. In the 20 plots from zone 4, there were 13 seedlings. In glades, pine seedlings fared better: 50 plots had 169 seedlings (MacRoberts & MacRoberts 1993). But the end result is the same in these two habitats. Irrespective of the number of pines that sprout and survive for a year or two, the vast majority eventually die. By the end of summer, after a few July and August droughts, very few pine seedlings remain.

Why do outcrop communities remain open? Several factors seem important (MacRoberts & MacRoberts 1990, 1993). First, edaphic conditions may be unfavorable. The soil itself appears to be nonabsorbant. We have excavated post holes in outcrops after two days of rain only to find that the soil is dry 10-15 cm below the surface. Also in outcrops, as in glades, there is an impermeable layer of rock. Further, even where soils are deep, the soil characteristics themselves impede woody plant establishment. The soil is high in calcium, which is known to deter growth in many plants including pines, and is stiff and seasonally droughty with high shrink-swell properties (Martin & Smith 1991: 64). Open areas are subject to very high summer temperatures and short droughts put severe stress on pine seedlings. But the fact that trees and midstory vegetation begin abruptly in zone 5 would indicate that there is something different between the soils in zones 4 and 5. The soil samples did not reveal what that might be.

During the course of this study we surveyed 36 outcrop communities in the Kisatchie District. These ranged in size from 0.1-2.0 ha (average 0.8 ha). Most contained all zones, but several consisted entirely or almost entirely of zone 4 (*i.e.*, were prairie-like) but were on slopes, not hilltops. That we were dealing

Table 5. Statistics on *Schoenolirion wrightii* populations.

Outcrop	Size (ha)	No. plants	Plant coverage (ha)	Cattle grazing
KG30-3	1.2	250	0.01	yes
KG30-5	1.2	150	0.01	yes
KG30-8	0.4	75	0.005	yes
KG36-1	0.4	1000	0.2	no
Sheard I	1.2	450	0.3	no

with an outcrop community at such sites was usually evident by the flora and also by the presence, discovered with minimal searching, of a rock ledge down slope, hidden by shrubby vegetation, that had not eroded out to pavement dimensions. Since all of these outcrops occurred at approximately 75 m above sea level, and since the rock layer was similar throughout, we assume that the same geological strata are repeated wherever outcrops occur.

NOTEWORTHY SPECIES

During the course of this study we found a number of species that deserve additional comment.

Schoenolirion wrightii. (*MacRoberts & MacRoberts 1901* [VDB]). This species is globally, federally, and state listed as rare (G3, C2, S1 Louisiana, S2 Texas) (see Nixon & Ward 1981; Orzell 1990; Grace 1993; for literature and recent reviews).

Between April 17, 1993, when we first discovered *Schoenolirion wrightii* on the Kisatchie National Forest and May 7, 1993, when it had ceased blooming and was becoming difficult to locate, we surveyed 19 outcrops in the western part of the Kisatchie Ranger District and found it at five sites (26%), often in large numbers (Table 5). The five populations are all located in T6N R8W a few miles north of Kisatchie, Louisiana. Within this area, the closest two populations are about 1 km apart; the most distant are 5 km apart.

In three outcrops *Schoenolirion wrightii* was confined to a small area. In the other two, it was much more widespread. In these latter two sites, cattle had been excluded for several years. In one of the outcrops where grazing occurred, the small population of *S. wrightii* was entirely grazed down just after it had set seed.

In an outcrop bisected by a road, a recent non-growing season prescribed burn (February 13, 1993) had burned the southern half. Although *Schoeno-*

lirion wrightii bloomed and set seed in both burned and unburned portions, plants appeared to be more prolific and larger in the unburned area.

We examined soils in the five outcrops in which *Schoenolirion wrightii* occurred. These soils are the same as those reported for zone 3 in Table 2 and can be as shallow as a few inches only.

Carex meadii. (*MacRoberts & MacRoberts 1889* [VDB]). Prior to the present study, this western species had been reported only once from Louisiana (Williams 1977; MacRoberts 1989), and specimens from three other parishes have recently been found in herbaria (Julia Larke, pers. comm.). It is currently ranked as rare (S1) in Louisiana. Although we made no special attempt to search for this species, we located three outcrops where it occurred in zone 4. Two of these are within 1 km of each other; the other is about 6 km distant.

Selaginella arenicola ssp. *riddellii.* (*MacRoberts & MacRoberts 1809* [VDB]). Riddell's spikemoss is rare (S1) in Louisiana. It occurs in zone 3 and is often associated with moss or lichens. We surveyed 36 outcrops in the Kisatchie Ranger District and found it, often in large mats, in five. The plants are easily dislodged by cattle trampling.

Talinum parviflorum. (*MacRoberts & MacRoberts 1759, 1780* [VDB]). This plant is rare in Louisiana (S1). At the beginning of this study, it was only known from three closely adjacent outcrops on the Kisatchie Ranger District. We found it in 24 of the 36 outcrops we surveyed, often in large numbers (more than 1000 plants). It grows almost exclusively in thin soils in slight depressions on the rock pavements in full sun (zone 3). It blooms in late afternoon. We collected soils in which *Talinum* grew from eight outcrops. All appear to be soils typical of zone 3.

Habranthus tubispathus (L'Herit.) Traub. (*MacRoberts & MacRoberts 2093* [VDB]). While not considered rare, we found this West Gulf Coastal Plain endemic at one outcrop, where it was abundant. It did not occur at KG30-2, 3, or 8.

It is found in barrens/glade/prairie habitat in southeast Texas (Orzell 1990).

DISCUSSION

During the course of this work, it became evident that we were sealing with a community that consisted of a sandstone outcrop and upslope a calcareous opening that would best fit the definition of prairie. But we have chosen not to call these upslope openings prairies after examining "true" calcareous prairies, which appear to be floristically somewhat different, are located on hilltops, not side slopes, and which are alkaline and usually more calcareous. Nonetheless, the upslope openings (zone 4) should be looked at as a type of calcareous prairie since their soils are calcareous and their flora is calciphilous.

The outcrop communities occurring in the Kisatchie National Forest appear to be very similar to the open ("prairie-like" or "barrens") communities described by Marietta & Nixon (1984), Bridges & Orzell (1989), Orzell (1990), and Mohlenbrock (1993) for east Texas. They are similar also to a number of barrens, glades, and prairies described for Arkansas and Missouri eastward. Notably similar appear to be the various cedar glades of Tennessee and Kentucky (Baskin & Baskin 1975, 1985, 1989; DeSelm 1986) and the "Black Belt" flora of Alabama (Robert Kral, pers. comm.).

We did not divide out floristic surveys according to zones. But clearly if we had done so, the different zones would have shown significant differences. Many plants that grow on the thin soils overlaying rock outcrops do not grow in the upslope zones, and vice versa. For example, *Talinum* and *Selaginella* are found only on or near rock pavements (zone 3); whereas the many composites, peas, and grasses typically occur in zone 4. It should be remembered, however, that what does grow on these outcrops is in part determined by the soils that erode down onto them from above and that, in the present case, these are usually calcareous. Since we have not had the opportunity to study outcrops with other soils upslope, we are not in a position to say how different they might be.

KG30-2, 3, and 8 were grazed. While this was not an ideal condition under which to make a floristic study, it did provide us with information on the effect of cattle on these communities. In a word, cattle have a disastrous effect. Not only do they crop the plants (they ate all the newly seeded *Schoenolirion wrightii* from one outcrop), but they crush and dislodge lichens and other plants, especially in zones 2 and 3. Trampling also initiates erosion in zones 1 and 4, where soils are so unstable (Martin *et al.* 1990) that massive erosion results, which not only sweeps away the soil above the rock shelf, but undermines the rock itself. The devastation caused by cattle shows that these communities require a good stable ground cover to keep them intact. Many of the outcrops on the Kisatchie National Forest that were once grazed are now free of cattle, and we are happy to report that the Forest Service has fenced the outcrops where this study took place.

One thing that did surprise us was that, although the three outcrops were grazed, we found no noticable difference in our floristic lists between them and outcrops that had not been grazed for some years. The only difference was that grasses in grazed areas were difficult to find and in short supply. Undoubtedly, a study using plots would reveal many differences in composition and number of species present between grazed and ungrazed sites.

Our work on open xeric rocky communities in the Kisatchie National Forest has convinced us that there are at least two distinct types (MacRoberts & MacRoberts 1993). This year's field work establishes that sandstone outcrops are clearly distinct from sandstone glades.

This finding clarifies some confusion that currently exists in the Louisiana

botanical literature. The community initially described by Smith (1988) was a sandstone outcrop, but when Martin & Smith (1991) described the major community types of the Kisatchie District of the Kisatchie National Forest, they reiterated Smith's 1988 description of the outcrop community, but exemplified it with a glade community. Hart & Lester (1993), without additional research or reference to the growing literature, have perpetuated the confusion by synonymizing glade and outcrop. Future community classifications should distinguish between sandstone outcrops and sandstone glades.

ACKNOWLEDGMENTS

The continuing cooperation and assistance of the staff of the Kisatchie National Forest have been instrumental in making this study, as in all our botanical research, possible. Especially to be thanked are Tom Fair, Susan Carr, and Viola Ritchie. Allan Tiarks, Southern Forest Experiment Station, answered some questions we had about the soil data. Financial support was provided, in part, by a Challenge Cost-Share Agreement with the Kisatchie National Forest. Robert Kral vetted a number of the plants, notably our *Carex* specimens. Julia Larke, Louisiana Natural Heritage Program, provided information on *Carex meadii* and other rare plant species. Jerry Baskin and Robert Kral made helpful comments on the paper.

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Phytologia (December 1993) 75(6):481.

ARENARIA GYPSOSTRATA B.L. TURNER, A NEW NAME FOR *A. HINTONIORUM* B.L. TURNER, NOT *A. HINTONIORUM* B.L. TURNER

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ABSTRACT

A new name (**Arenaria gypsostrata**) is required to substitute for *A. hintoniorum* which is a later homonym of a previous *A. hintoniorum*.

KEY WORDS: Caryophyllaceae, *Arenaria*, México, gypsophile

Arenaria gypsostrata B.L. Turner, *nom. nov.* Based upon *Arenaria hintoniorum* B.L. Turner, Phytologia 75:406. 1993 [Feb 1994]. Not *Arenaria hintoniorum* B.L. Turner, Phytologia 7259. 1992.

In my overzealous effort to eponymise the remarkable Hinton family, a lapse permitted the nomenclatural mistake corrected here, for which my apologies to the Hinton family and the broader systematic community.

CORRECTIONS AND ADDITIONS

Volume 74, issue 3, page 178, line 4 of abstract, "Fabanae" should not have a hyphen.

Volume 75, issue 2, inside front cover, D.M. Sutherland was omitted as an author of the paper entitled " Chromosome numbers for *Dalea* species (

FabaceaeFabaceae) from southwestern New Mexico and southeastern Arizona.

Volume 75, issue 3, inside front cover, the paper by MacRoberts & MacRoberts begins on page 247, not page 248.

Volume 75, issue 4, the running heads on all even numbered pages should read "P H Y T O L O G I A 74(5):xxx-xxx October 1993" rather than "P H Y T O L O G I A 74(4):xxx-xxx October 1993".

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):277-280." rather than "*Phytologia* (October 1993) 74(4):277-280."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):281-324." rather than "*Phytologia* (October 1993) 74(4):281-324."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):325-329." raıher than "*Phytologia* (October 1993) 74(4):325-329."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):330-332." rather than "*Phytologia* (October 1993) 74(4):330-332."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):333-335." rather than "*Phytologia* (October 1993) 74(4):333-335."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):336-338." rather than "*Phytologia* (October 1993) 74(4):336-338."

Volume 75, issue 4, page 277, line 1 should read "*Phytologia* (October 1993) 75(4):339-340." rather than "*Phytologia* (October 1993) 74(4):339-340."

INDEX TO AUTHORS, VOLUME 75

Phytologia (December 1993) 75(6):484-512.

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New taxa described in this volume are indicated in bold face type.

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